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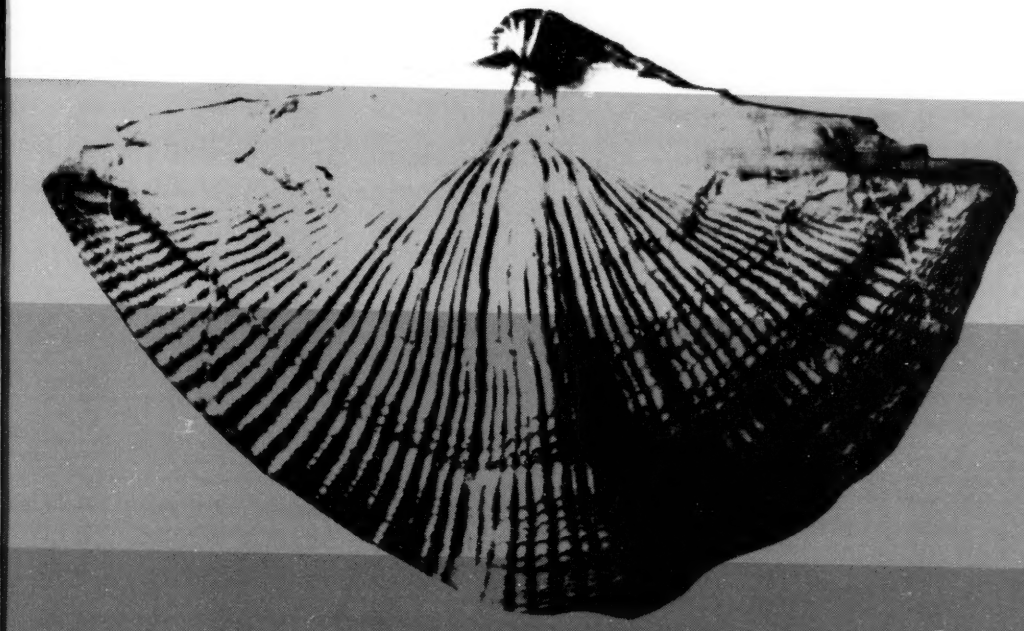

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Since Russian geological terminology is based on concepts often different from those in English, making distinctions not recognized in English and vice versa, the following translations of Russian stratigraphic and other terms have been somewhat arbitrarily adopted:

Russian	gruppa	= English	'eratem'
"	seriya (when named)	= "	'group'
"	sistema	= "	'system'
"	otdel	= "	'series'
"	yarus	= "	'stage'
"	svita (chronostratigraphic)	= "	'formation'
"	gorizont	= "	'(stratigraphic) horizon'
"	pachka	= "	'unit'
"	platforma, molodaya	= "	'platform'
"	platforma, drevnyya	= "	'craton'
"	kraton	= "	'craton'

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LATE VENDIAN HELICOID FILAMENTOUS MICROFOSSILS

M. B. Burzin

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Abstract: Five suprageneric groups of helicoid microfossils from the Upper Precambrian are erected based on the anatomy of the filament: (1) *Obruchevella* group - trichrome with tubular sheath; (2) *Volyniella* - empty filamentous envelope without cellular structure; (3) *Boruokia* - trichome; (4) *Grypania* - taeniate thallus; and (5) *Spirillopsis* - sheath with pyrite crystal inside it. Genera *Obruchevella* Reitlinger and *Volyniella* Assejeva and species *O. parva* Reitlinger and *V. valdaica* Assejeva are revised and redescribed. *Spirillopsis* n. gen. and *S. pyritofera* n. sp. are described.

Основываясь на анатомическом строении нитей среди позднедокембрийских спирально-свернутых микрофоссилий выделено пять надродовых групп. 1 группа (типовой род – *Obruchevella*) – трихом в трубчатом чехле; 2 группа (типовой род – *Volyniella*) – нитевидные оболочки без клеточной структуры; 3 группа (типовой род – *Boruokia*) – "голый" трихом без чехла; 4 группа (типовой род – *Spirilliopsis*) – трубчатые чехлы, заполненные кристаллами пирита. Переописаны и уточнены диагнозы родов *Obruchevella* Reitlinger и *Volyniella* Assejeva и видов *O. parva* Reitling и *V. valdaica* Assejeva. Описан новый род *Spirilliopsis* и новый вид *S. pyritofera*.

• • •

Precambrian micropaleontologists often work with fragments of different organisms that belonged to different communities. This presents a challenge in recognizing different parts and forms of preservation of the same organisms. Problems of classification increase because of a limited number of morphological features preserved, and of a high probability of a frequently repeated and parallel (that is, independently, in different taxa) derivation of the identical morphological feature. All this makes recognition of groups, not only by morphological similarity but also on phylogenetic basis next to impossible. As a result, among numerous formal microfossil groups, we can distinguish only a few "natural groups," of which the best example is the *Obruchevella*-like microfossils - helicoid organic-walled, silicified filaments, calcareous algae, and phosphatic fossils.

Five new suprageneric groups of helicoid filamentous microfossils are distinguished, based on anatomy of the filament and the ecology. This new approach to the classification of helicoid Upper Precambrian forms has been possible only due to a unique rich collection of organic-walled microfossils that I found in the Rozniche Formation (Upper Vendian, Redkino Horizon)

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from Volhynia (Ukraine), from Borehole No. 1547 of the Rovno Geological Prospecting Expedition of the Commercial Amalgamation "Sevukrgeologia." In this collection there are representatives of *Obruchevella* Reitlinger, *Volyniella* Assejeva, 1974, *Buruokia* Kolosov, 1984, and *Spirillopsis* Burzin, gen. nov. Their excellent preservation permitted investigation of their anatomy, taphonomy, and paleoecology, and allowed me to separate characters of the living structure of filament from those of postmortem alteration. As all genera are organic-walled microfossils, it gives a unique opportunity to study the anatomy without the usual problem of Precambrian methodology of comparing microfossils with different types of preservation and from different conditions.

This investigation has been supported by the Russian Foundation for Fundamental Investigation, Project No. 93-05-08816, "Neoproterozoic Geobiological Events."

Diversity of Helicoid Microfossils

Only a few diagnostic features can be used for examining the diversity of these microfossils. Traditionally the characteristics of the spiral were the principal features for classification, but now we can use the anatomy of the filament and the ecological peculiarities.

1. Characteristics of Spiral

Some representatives of *Eomycetopsis* (Sergeev, 1992, pl. XIX, fig. 6) and *Botuobia* (Kolosov, 1984, pl. IX, fig. 1) have curved and coiled filaments.

A two-dimensional (flat) spiral is characteristic for filaments identified as *Helmintoidichnites* (Sokolov, 1977, fig. b on p. 436; Gnilovskaya, 1979, pl. XVI, figs. 2, 6).

Cochleatina Assejeva, 1983, has a ribbon-like structure that is complex and compound, and curved to form a regular two-dimensional (flat) spiral, but the surface of this ribbon is parallel or less than 90° to the axis of coiling.

The helicoid makes only 1-2 coils, which is characteristic for *Boruokia, Tubulosa* Assejeva, 1982, *Anabaenidium* Schopf, 1968, and *Jiangispirellus* Peel, 1988.

Representatives of *Tortunema* Hermann, 1976, and *Glomovertella* Reitlinger, 1948, differ from others in that the coiled structure is formed not by a solitary filament, but by a tuft of filaments.

The type species of *Heliconema* Schopf, 1968 — *H. australiensis* Schopf, 1968 — is not a helicoid, as claimed by A. H. Knoll (1992). However, three other species previously in this genus, "*H.*" *turuchanica* Hermann, 1981, "*H.*" *uralense* Jankauskas, 1980, and "*H.*" *bullosa* Alison et Awramik, 1989, are characterized by a spirally coiled filament. As a new genus has not been described yet, I use the name "*Heliconema*" for these three species.

The genera *Obruchevella, Volyniella, Spirillopsis* gen. nov., *Avictuspirulina* Strother, Knoll et Barghoorn, 1983, *Glomerula* Singh et Shukla, 1981, *Spirellus* Jiang in Luo et al., 1982, and *Grypania* Walter, Oehler et Oehler, 1976, emend. Walter, Du Rulin et Horodyski, 1990, are

characterized by regular cylindrical isodiametric helicoid spirals, except that on some specimens the diameter of the helix may sometimes decrease toward the ends of the spiral. Characteristics of spirals were investigated by J. S. Peel (1988) and C. Mankiewicz (1992) for *Obruchevella* and some relatives. The similarity of these characteristics is so great, that some authors (e.g., Golovenok, 1989) combined some of these genera and defined the genus *Obruchevella* extremely broadly.

2. Filament Anatomy

Several types of helicoid filament of anatomic structure may be established.

Obruchevella, Glomovertella, "*Heliconema,*" and *Glomerula* usually have empty isodiametric tubular sheaths with open apices. This anatomy indicates that filaments of these genera may consist of solitary trichomes with disk-shaped or cylindrical vegetative cells, surrounded by tubular sheaths. Remains of cells and trichomes were found in some *Obruchevella* (Song, 1984; Knoll and Ohta, 1989). It can be assumed that these forms have anatomy similar to the modern cyanobacteria *Lyngbya-Phormidium-Plectonema* group, but traditionally *Obruchevella* was compared with modern cyanobacteria *Spirulina*, whose sheath formation is never pronounced.

Boruokia, Tortunema, Anabaenidium and *Jiangispirellus* have only a "naked" trichome without a sheath; cells of the trichome are vegetative, disk-shaped or cylindrical and not separated by deep constrictions. Cells may be distinguished on all parts of the trichome or only on its terminations (*Tortunema*). Modern cyanobacteria *Oscillatoria* and *Spirulina* groups have the same anatomy, but the size of *Jiangispirellus* is too large, as compared with the prevailing size of modern cyanobacteria.

Volyniella, Avictuspirulina and *Spirellus* have a filamentous envelope without a cellular structure, terminally closed. Three interpretations of this morphology may be supported: (1) The filamentous envelope is made from the exterior of the cell wall. Parts of the cell wall that formed the cross wall were thinner and rapidly disappeared, possibly due to physiology or to aging of the filament. (2) The envelope was a typical cyanobacterian trichome during life, but the cross walls were selectively destroyed during burial, possibly due to the destruction of gas vacuoles as in modern planktonic filamentous cyanobacteria. (3) The filament structure is nontrichomal but siphonal, like the thallus. Modern cyanobacteria with this thallus are unknown, but some eukaryotic algae have siphonal thalli. I think the third interpretation is most improbable, because the majority of these fossils with such anatomy are obviously too small to be eukaryotic; only two species of *Volyniella* and one of *Spirellus* are large enough to be potentially considered as eukaryotic. The first interpretation is more probable, but it is strange that in my rich collection of *Volyniella valdaica*, cellular structures were not found. Therefore, in my opinion, the second interpretation is least contradictory, and provides a good correlation with the taphonomy of these genera.

There are some doubts about the anatomy of *Tubulosa* which is very similar to *Volyniella* but with a wrinkled envelope. E. A. Assejeva (1982) has noted in her description of the genus that the filament of the type species has a tubular structure with open apices. Such a structure is typical of *Obruchevella*, but there is a question of whether Assejeva really saw open apices or only broken fragments of filamentous envelopes, as she did not observe closed terminations of *Volyniella valdaica* (Assejeva, 1974).

Grypania are known only as carbonaceous remains and imprints (Walter et al., 1990). *Grypania* apparently has a taeniate thallus with rounded terminations, whose cellular structure is unknown. The size and type of preservation of *Grypania* is similar to that of some vendotaenids (Gnilovskaya, 1988) i.e., eukaryotic macroscopic, possibly multicellular ("meta-phytic"), algae.

The new genus *Spirillopsis* has an extraordinary anatomical structure. A thin tabular sheath whose terminations are unknown contains pyrite crystals. Crystals placed regularly in the form of a chain may fill all the inner cavity of the sheath. Sometimes rare pyrite crystals are found inside the *Obruchevella* sheath (Sergeev, 1992, pl. XXV; Mankiewicz, 1992, fig. 8). The interpretation of the presence of pyrite crystals inside the envelope will be examined below. I think the most probable interpretation is that the pyrite crystals are diagenetic pseudomorphs after sulphur grains were formed within cells of chemoautotrophic microorganisms. Thus, *Spirillopsis* may be compared with modern filamentous cyanobacteria of the Beggiatoaceae family. The presence of pyrite crystals inside the *Obruchevella* sheath may indicate the presence of sulphur grains inside its living cells, and thus it may be explained by analogy with some modern oscillatorian cyanobacteria which can carry out facultative anaerobic photosynthesis (Stanier et al., 1981).

3. Ecology

Reliable ecological interpretations may be made only for *Obruchevella, Volyniella, Boruokia*, and *Spirillopsis*.

Obruchevella is known from cherts as either a minor component of cyanobacterial mats (Shenfil, 1980; Liu et al., 1984; Zhang, 1984; Ogurtsova and Sergeev, 1987), or of mat-like colonies like those from the Upper Vendian Tinnaya Formation of Siberia (Reitlinger, 1948, 1959; Kolosov, 1977; Luchinina, 1981). As organic-walled microfossils, *Obruchevella* are frequently in clusters and have an excellent and undistorted preservation which may indicate an autochthonous burial. Calcareous forms are found in the *Obruchevella* genus, all of which suggest the benthic mode of life of *Obruchevella*, like some modern cyanobacteria.

Volyniella and *Boruokia* are known only as organic-walled microfossils from mudstones. They are found only as solitary specimens, their spiral shape is always distorted, which is evidence of an allochthonous burial and, thus, a planktonic life.

The new genus *Spirillopsis* was found only with mats of filamentous sulphur bacteria *Zinkovioides inclusis* Hermann, 1985 (Burzin, 1993) in samples where benthic cyanobacteria and filamentous algae are known only as fragments, and thus are allochthonous remains. Usually envelopes and sheaths of these allochthonous forms have an incrustation of pyrite crystals due to activity of sulphur-reducing bacteria, but I have never seen pyrite incrustations on sheaths of *Spirillopsis* and *Zinkovioides*. This allows me to conclude that *Spirillopsis* lived beneath the photic zone of the paleobasin with plentiful organic matter, planktonogenic or transported from shallow waters. Modern Beggiatoaceae have the same mode of life.

Classification of Helicoid Filamentous Microfossils

Obruchevella Group. This group includes forms with tubular sheaths, sometimes with inner

trichomes observed. The filament is coiled to form a regular cylindrical isodiametric spiral; coils of the spiral usually closely connect with one another, and sometimes the capsule enveloping the entire helix is observed. The thallus of these forms is similar to the modern filamentous oscillatorian cyanobacteria *Lyngbya-Phormidium-Plectonema* group, whose filament consists of a solitary trichome surrounded by a tubular sheath. They were benthic cyanobacteria-like organisms, some forms were mat-building organisms. Only this group includes calcareous algae. Composition: *Obruchevella, Glomovertella, "Heliconema,"* and *Glomerula.*

Volyniella Group. This group includes forms with the filamentous envelope closed at terminations, and without cellular structure. The spiral is frequently distorted, sometimes recoiled. Such an envelope cannot be identified as a tubular sheath; more possibly it is an outer wall of the trichome, because only the outer parts of walls of cells that composed the trichome have been preserved, while cross walls have been destroyed. The same type of preservation is known for some straight filaments of *Leiotrichoides*. They were, possibly, planktonic cyanobacteria-like organisms, perhaps with gas vacuoles inside the cells or, less probably, planktonic siphonal filamentous algae. Composition: *Volyniella, Avictuspirulina, Spirellus* and *?Tubulosa.*

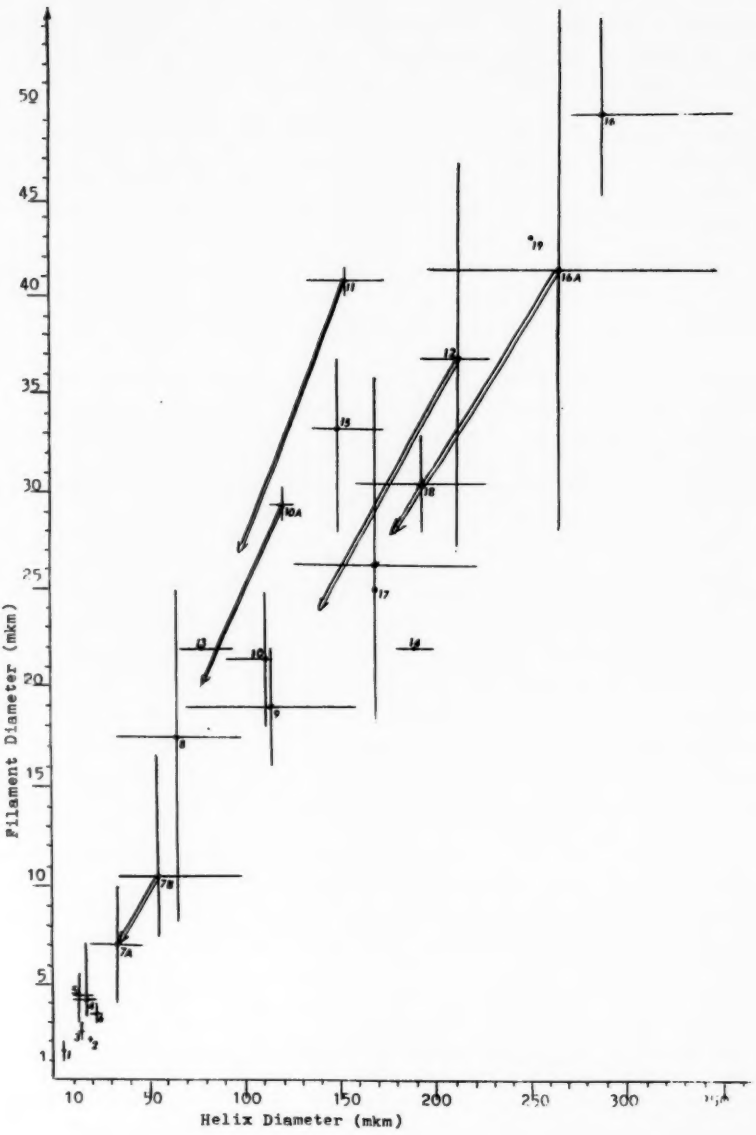
Buruokia Group. This group includes forms with a "naked" trichome without a sheath. Cells that compose the trichome are disk-shaped and vegetative (no heterocysts or akinetes). The filament is coiled to form a helicoid spiral with 1-2 coils. The thallus of these forms is similar to modern filamentous oscillatorian *Oscillatoria* and *Spirulina* groups. They were planktonic cyanobacteria-like organisms. Composition: *Boruokia, Tortunema, Anabaenidium*, and *Jiangispirellus.*

Grypania Group. This group includes forms with a taeniate thallus, known only as carbonaceous remains and imprints. Their cellular structure is unknown. Based on preservation (spirals are sometimes recoiled and distorted) and taphonomy (usually only solitary specimens have been found) it is definite they were planktonic. Composition: *Grypania.*

Spirillopsis Group. This group includes forms with a thin tubular sheath containing pyrite crystals, which may be arranged either singly in a chain or in clusters filling the entire sheath. The filament is coiled in a helix which, evidently, was regular, cylindrical and isodiametric in life, as the helix was not rigid, it could be easily deformed, and uncoiled before becoming a flat concentric spiral. This group does not includes *Obruchevella*, which also sometimes has pyrite crystals inside their typical tubular sheath. *Spirellus* and *Zinkovioides* (mat-building form with a thin straight tubular sheath containing pyrite crystals) are undoubtedly relatives, and it is possible that they may be benthic filamentous sulphur bacteria like modern Beggiatoaceae. Composition: *Spirillopsis* gen. nov.

Systematic Paleontology

Genera *Obruchevella* Reitlinger and *Volyniella* Assejeva and species *O. parva* Reitlinger and *V. valdaica* Assejeva are revised and redescribed, based on new data from the Upper Vendian of Volhynia and Ukraine. *Spirillopsis* n. gen. and *S. pyritofera* n. sp. are described. This collection of specimens and slides is housed in the Paleontological Institute of the Russian Academy of Sciences (PIN), No. 4328a.


Filament Diameter (mkm)
Helix Diameter (mkm)
50
45
40
35
30
25
20
15
10
5
1
10
50
100
150
200
250
300

Obruchevella Group

Obruchevella Reitlinger, 1948, emend. nov.

Obruchevella: Reitlinger, 1948, p. 78; 1959, p. 21; Vologdin, 1958, p. 407; Luchinina, 1975, p. 29; Kolosov, 1977, p. 73; 1984, pp. 57-58; Yakshin and Luchinina, 1981, p. 29; Chuvashov et al., 1985, p. 78; Pjatiletov, 1986, pp. 150-151 (part.); Jankauskas et al., 1985, pp. 112-113 (part.); Golovenok and Belova, 1989, pp. 191-192; Golovenok, 1989, p. 43 (part.); Song, 1984, pp. 181, 183; Bengtson et al., 1990, p. 20; Gorodnichev and Drobkova, 1991, pp. 123-124; Sergeev, 1992, pp. 89, 112; Mankiewicz, 1992, pp. 717-724; Knoll, 1992, pp. 755-758.

Lukashevella: Vologdin, 1958, p. 408.

Kordeella: Vologdin, 1958, p. 407.

Type species. *Obruchevella delicata* Reitlinger, 1948

Diagnosis. Filamentous remains of empty hollow sheaths and trichomes with or without sheaths. When cellular structure known, trichome uniseriate, cells discoidal or square-cylindrical. Diameter of filaments ranging from 1 to 50 (when flattened) μm. Trichome terminations not known. Sheath thin or thick, smooth or striated, often calcareous or, more seldom, phosphatized, tubular, open on the ends, not tapering at terminations. Filament coiled as regular cylindrical isodiametric helix with diameter of 3.5-23 (when flattened) μm; helix coils touching one another as if forming solid "tube" of coils, or possibly stretched. Helix pitch equal to filament's diameter or up to twice larger. Helix comprising 3-18 coils; length of helix several times its diameter.

Preservation. This genus is known as organic-walled or mineralized fossils. Only the tubular sheath, with no traces of trichome inside, may be preserved in an organic-walled form. Silicified microfossils, calcareous algae, and phosphatized remains are known in mineralized form. Only empty sheaths are mainly preserved as silicified microfossils, but three species from Yunnan Province, China (Song, 1984), have trichomes preserved in or without sheaths. Sometimes, in

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Fig. 1. Variation of *Obruchevella* as a function of helix and filament diameter. Horizontal and vertical bars denote range in size. List of species: 1 - *O. pusilla* (Golovenok and Belova, 1983); 2 - *O. blandita* (Shenfil, 1980); 3 - *O.* sp. (Ogurtsova and Sergeev, 1987) = *O. exilis* (Sergeev, 1992); 4 - *O. condensata* (Liu et al., 1984; Golovenok et al., 1989); 5 - *O. minor* (Zhang, 1984); 6 - *O. parvissima* (Song, 1984; Luo et al., 1984; Ogurtsova and Sergeev, 1987; Sergeev, 1992); 7*a* - *O. parva* (silicified microfossils and phosphatic remains); 7*b* - *O. parva* (organic-walled microfossils); 8 - *O. delicata*; 9 - *O. meishucunensis* (Song, 1984; Luo et al., 1984; Ogurtsova and Sergeev, 1987; Sergeev, 1992); 10 - *O. ditissima* (Yakshin and Luchinina, 1981; Gorodnichev and Drobkova, 1991); 10*a* - *O. ditissima* (Kolosov, 1985); 11 - *O. crassa* (Kolosov, 1984; Jankauskas et al., 1989); 12 - *O. inviolata* (Kolosov, 1984; Jankauskas et al., 1989); 13 - *O. spiralis* (Kolosov, 1985); 14 - *O. olchinica* (Gorodnichev and Drobkova, 1991); 15 - *O. magna* (Golovenok et al., 1989); 16 - *O. gigantea* (Golovenok et al., 1989); 16*a* - *O.* cf. *O. gigantea* (Golovenok et al., 1990); 17 - *O.* sp. (Wang et al., 1983); 18 - ?*O.* sp. (Knoll and Ohta, 1988); 19 - *O.* spp? (Cloud et al., 1979). The original dimensions before flattening for organic-walled microfossils are indicated by arrows.

silicified microfossils a matrix or capsule around the sheath envelops the entire helix; it may possibly be a fossilized extracellular envelope. When preserved as calcareous algae, filament structures cannot be discerned, and there is only a thin or thick carbonate sheath with a microgranular microstructure. In phosphatic mineralization, the phosphate layer evidently formed around the organic sheath, or, more often, on the outer and sometimes on the inner surfaces of the carbonate sheath; this results in formation of a tubular phosphatic sheath or of a sheath and an inner mold of the carbonate sheath cavity corresponding in size to the filament's diameter. Bending of the axis of coiling, a change in helix pitches towards its ends, and an uncoiling of the helix, are postmortem changes (Song, 1984; Ogurtsova and Sergeev, 1989). Usually the preservation suggests their predominantly autochthonous burial and, hence, a benthic mode of life; *Obruchevella* probably formed benthic colonies and mat-like structures.

Species composition. The genus comprises 14 species which differ mainly in size of the filament and the helix (fig. 1). Only one species has a striated, rather than a smooth, sheath.

The following species of *Obruchevella* are the smallest: *O. pusilla* Golovenok et Belova, 1983 (diameter of filament 1-1.65 μm, diameter of helix - 4-5 μm, pitch - 2-2.2 μm) from Middle-Upper Riphean Valyukhta Formation of Patom Uplift, Siberia (silicified microfossils); *O. blandita* Shenfil, 1980 (diameter of filament - 2.1-2.2 μm, of helix - 18-20 μm) from Upper Riphean Seryy Klyuch Formation of Yenisey Ridge, Siberia (silicified); *O. condensata* Liu et al., 1984 (diameter of filament - 3-7 μm, of helix - 10-22 μm, pitch - 2.5-5.5 μm) from ?Upper Riphean Jindingshan Formation of Jiangsu Province, China (silicified), and Lower Vendian Buton Formation of Serebryanka Group from Urals, Russia (phosphatized) and related *O.* sp. (Ogurtsova and Sergeev, 1987) (diameter of filament - 2.8-3.3 μm, of helix - 16 μm, pitch - 3.3-5.6 μm) from ?Upper Riphean-Lower Vendian Chichkan Formation of Lesser Karatau, Kazakhstan (silicified); *O. minor* Zang, 1984 (diameter of filament - 3.5-5.5 μm, of helix - 10-19.5 μm, pitch - 6-9 μm) from Sinian (?Lower Vendian) Doushantou (=Toushauntou, = Toushan) Formation, Hubei Pronvince, China (silicified); *O. parvissima* Song, 1984 (diameter of filament - 3-4 μm, of helix - 20-24 μm, pitch - more than 4 μm) from Early Cambrian Yuhucun Formation (Zhongyicun Member) of Yunnan Province, China, and Chulaktau Formation of Lesser Karatau, Kazakhstan (silicified).

The next species by size is *O. parva* Reitlinger, 1959 (diameter of filament - 4-10 μm, when flattened - 6.6-16.6 μm; diameter of helix - 19-47 μm, when flattened and distorted - 35-102 μm; pitch equals 1-2 diameters of filament). This species is known from the Upper Precambrian black carbonate-pelite unit of Prins Karls Forland, western Svalbard (silicified); from the Upper Vendian Tinnaya Formation of Nokhtuysk section, Siberia (silicified); from Upper Vendian Zinkovo beds of Yaryshevka Formation from Podolia, and Rozniche Formation from Volhynia, Ukraine (organic-walled); from Upper Vendian of Finland (described as *Volyniella cylindrica* Tynni et Donner, 1980) (organic-walled); from ?Vendian - ?Cambrian of Irkutsk Region, Siberia (silicified); from Early Cambrian Chulaktau Formation of Lesser Karatau, Kazakhstan (including samples determined as *O. delicata* by Ogurtsova and Sergeev); from Meishucum and Yuhucum formations of Yunnan, China (silicified); and from Portfjeld Formation of Peary Land, Greenland (phosphatic).

The type species of *O. delicata* Reitlinger, 1948 (diameter of filament - 10-25 μm, thickness of calcareous or phosphatic sheath - 1-5 μm, diameter of helix - 32-100 μm) are known as calcareous algae, silicified microfossils, and phosphatic remains from the Upper Vendian Tinnaya Formation from Nokhtuysk section, Siberia; from Early Cambrian Meishucum and Yuhu-

cun formations from Yunnan, China; from Atdabanian of eastern Anabar Uplift (Rassokha River), middle parts of the Lena River and eastern Sayan, Siberia; from Atdabanian-Botomian of Tuva; from Botomian of middle parts of Lena River, Siberia, western Mongolia, and Northern Australia; from Upper Cambrian or Ordovician from northern Siberia (described as *O. sibirica* Reitlinger, 1959) and Devonian of western Siberia. *O. spiralis* has a very similar size (diameter of filament - about 22 μm, of helix - 66-96 μm), and is from the Lower Ordovician Philipsburg Group from Quebec, Canada. *O. meishucunensis* Song, 1984 (diameter of filament - 16-22 μm, of helix - 68-162 μm) is from Lower Cambrian Yuhucun Formation from Yunnan Province, China, and Chulaktau Formation of Lesser Karatau, Kazakhstan (silicified). *O. ditissima* Schiritzin et Yakshin, 1981 (diameter of filament was indicated as 18-25 μm, of helix - 110-115 μm) is known from ?Vendian Martynkino Formation from Kuznetskiy Alatau, Siberia (samples from Martynkino Formation have unique striated sheath); from ?Vendian Olchinsk Formation from Irkutsk Region, Siberia and Lower Vendian Kursov Formation from western Yakutia (Kolosov, 1985). *O. olchinica* Gorodnichev et Drobkova, 1991 (diameter of filament - 22 μm, of helix - 180-200 μm from ?Vendian Olchinsk Formation from Irkutsk Region, Siberia (? calcareous algae) has a similar diameter of filament, but broader helix.

Four species are the largest: *O. magna* Golovenok et Belova in Golovenok et al., 1989 (diameter of filament - 28-37 μm, of helix - 135-175 μm) from Lower Vendian Buton Formation from Urals, Russia (phosphatic); *O. crassa* Kolosov, 1984 (diameter of filament - 40-41.6 μm, of helix - 135-175 μm) from Lower Vendian Kursovka Formation from western Yakutia (organic-walled); *O. inviolata* (Kolosov, 1984) originally described as *Volyniella inviolata* (diameter of filament - 27-46.8 μm, of helix - up to 200-270 μm) from Kursov and Iktekh formations from western Yakutia, Siberia (organic-walled); and *O. gigantea* Golovenok et Belova in Golovenok et al., 1989 (diameter of filament - 45-55 μm, of helix - 275-360 μm) from Lower Vendian Buton Formation from Urals, Russia (phosphatic), and very unusual pyritized specimens identified as *O.* cf. *O. gigantea* (Golovenok et al., 1990) (diameter of filament - 2-56 μm, of helix - 198-350 μm) from Lower Vendian Partzino Formation from Nepa-Botuoba Region (western Yakutia), Siberia (originally organic-walled microfossils).

Comparison. *Obruchevella* differs from *Volyniella* Assejeva, 1974, in its preservation as an empty sheath or, more seldom, as a trichome with or without a sheath, but not as a filament-like envelope closed at the terminations and containing no inner structures, and also in the helix length exceeding, as a rule, several times its diameter. Different modes of life are possible too: *Obruchevella* - benthic, and *Volyniella* - planktonic. *Obruchevella* differs from "*Heliconema*" Schopf, 1968, in the type of helix: *Obruchevella* has a cylindrical hollow helix, and "*Heliconema*" has a screw-like helix; its diameter exceeds that of the filament by no more than two. From *Anabaenidium* Schopf, 1974, *Tortunema* Herman, 1976, and *Boruokia* Kolosov, 1984, it differs in the filament structure and coiling of the filament in a regular cylindrical helix, not by just one or two turns or a concentric helix. It differs from *Jiangispirellus* Peel, 1988, in its considerably smaller size and the structure of the filaments. In phosphatized specimens, the cellular structure is never observed in *Obruchevella*, and this may indirectly indicate fundamental differences in the degree of organization in these two genera. *Obruchevella* differs from *Spirellus* Jiang in Luo et al., 1984, in the preservation of the filament as an empty tubular sheath, or, more seldom, a trichome with or without a sheath, but not as a filamentous envelope closed at the terminations, and in a considerably smaller size. It differs from *Spirillopsis* gen. nov. in the absence of pyrite crystals inside the sheath and by a much more compact helix.

Obruchevella parva Reitlinger, 1959 emend. nov.

Pl. I, figs. 1-3, 4A; Pl. III, fig. 1

Obruchevella parva: Reitlinger, 1959, p. 21, pl. VI, figs. 1, 2; Kolosov, 1977, pp. 73-74, pl. IV, fig. 2; 1982, pl. XVI, figs. 1*a*, *b*; Cloud et al., 1979, pp. 87-89, figs. 5J-K; Yakshin and Luchinina, 1981, p. 30, pl. X, figs. 1-3; Golovenok and Belova, 1983, p. 1464, fig. 1; 1989, p. 193, figs. 1-3; Wang et al., 1983, p. 159, figs. 5(1-4), 6(8); Song, 1984, p. 183, figs. 3(1-3, 8); Song et al. in Luo et al., 1984, p. 19, figs. 2-4, 10, 16; Ogurtsova and Sergeev, 1987, p. 60, pl. I, figs. 1-3, 5-9, 12; Knoll and Ohta, 1988, p. 63, fig. 3A-D; Gorodnichev and Drobkova, 1991, p. 125, pl. II, fig. 2; Sergeev, 1992, p. 89, pl. XXIV, figs. 5, 6, 11, pl. XXV, figs. 1-3, 5, 6; Knoll, 1992, p. 756, pl. I, figs. 2, 5; Burzin; 1993, pl. II, fig. 3.

Obruchevella delicata: Ogurtsova and Sergeev, 1989, p. 60, pl. I, fig. 4; Sergeev, 1992, pp. 89-90, pl. XXV, fig. 7.

Volyniella cylindrica: Tynni and Donner, 1980, p. 13, fig. 9, pl. V, figs. 47-63.

Obruchevella cylindrica: Jankauskas et al., 1989, p. 119 (part.), non pl. XXVI, fig. 15.

Volyniella jampolica: Assejeva, 1974, pl., fig. 9.

Volyniella valdaica (part.): Assejeva, 1976, pl. XVIII, fig. 3; 1983, pl. XII, fig. 4.

Holotype. Geological Institute, Russian Academy of Sciences, No. 3434/32 (thin section, silicified microfossil); Lena River, Nokhtuysk region; Upper Vendian, Tinnaya Formation (Reitlinger, 1959, pp. 21, 53, pl. VI, fig. 1, the longest specimen).

Description. The sheath is tubular, smooth, thin, without trichomes inside, and with constant width. The sheath is coiled into a regular cylindrical isodiametric helix. The coils of the helix are adjacent to each other (a helix pitch is equal to the diameter of the filament) and form a solid tubular construction. The coils are arranged freely but the helix's regularity is never broken, or they are enveloped by the matrix which is, evidently, a fossilized mucus. Helix coils number from 3 to 18, usually 6-9.

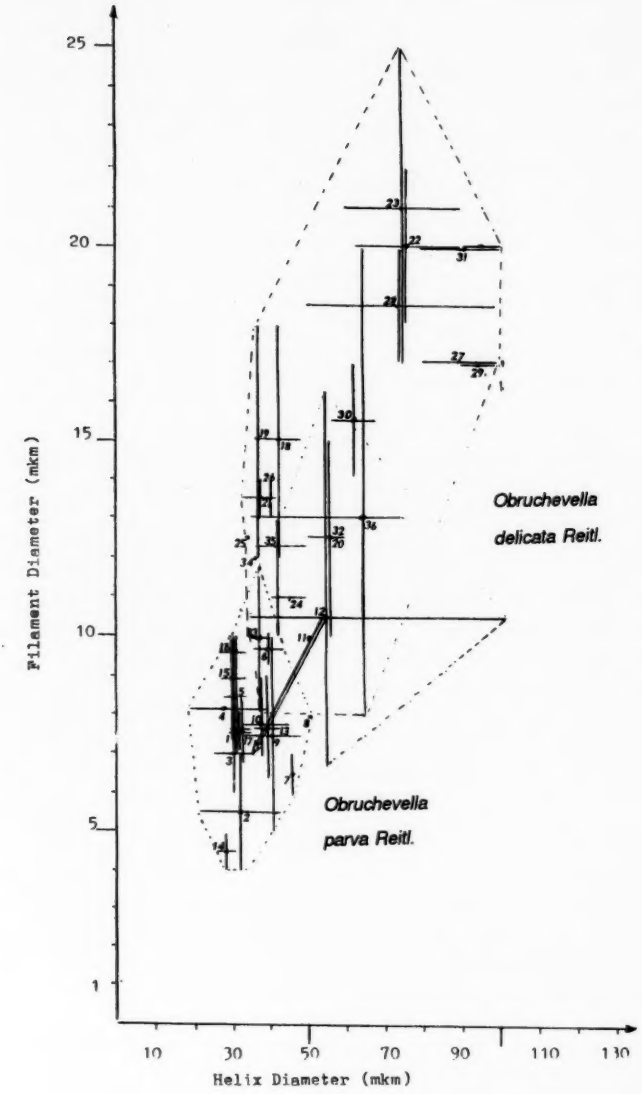
Preservation. This species is known both in a mineralized and organic-walled form. When mineralization is silicified, then microfossils are formed in cherts, they preserve the sheath, and sometimes a mucous matrix is seen around the sheath. Phosphatized remains in which the phosphate tube is formed around the organic sheath are known, and sometimes a phosphatic mold of the inner sheath's cavity is formed. The species has never been found in a calcified state. In all forms of preservation, a regular cylindrical shape of helix is observed, although in forms with an extracellular envelope around the sheath, the coils do not touch one another. The samples from the East European Platform have only an organic-walled preservation; both the sheath itself and the helix formed by it underwent a flattening during the lithification of the sediment, but they were deformed in different ways, depending on the orientation of the specimen and its parts. The peculiar deformation of the fossils is connected with the considerable interrelation of the helix coils in such a way that, in flattening, the helix acts like a thick-walled "tube" whose walls are made by the coils of the sheath. When the flattening occurred parallel to the axis of coiling, the diameter of the helix increased about 1.5 times, but that of the sheath was

distorted in different ways in different parts of the helix. Along the "tube's" edge are clearly distinct sections of turns that are distorted but not completely flattened. When the helix is flattened perpendicular to the axis of coiling, the diameter of the helix is not distorted, and the width of the sheath increases 1.5 times. If the helix is oriented at an angle to the direction of flattening or its parts have different orientation (which rarely occurs), then intermediate forms of preservation and parameter distortions are observed; usually, however, the helices are flattened on the plane, and the diameter of the flattened helix appears to be constant throughout the helix's length. In flattening, no stretching of the coils or a distortion of the helix's shape is observed. Sometimes an illusion occurs at the point of overlapping of coils, where the helix consists of annular elements with pointed ends, as noted by Tynni and Donner (1980, pp. 13, 14, fig. 2). The majority of specimens are dark-colored because of protoplasm preserved in the sheath, and distributed by the homogeneous layer throughout the entire length of the sheath. There are light-colored specimens with no protoplasm inside, and the sheath is not too thick. The forms are found in isolation in groups where specimens are connected only by a mere contact, in masses of decayed organic matter, or arranged in one layer in a thin, transparent and homogeneous sapropel-like film which is probably the common extracellular matrix of the fossilized colony. The degree of preservation and nature of distribution of the fossils suggest a predominantly autochthonous burial of these specimens and, correspondingly, a benthic mode of life. No pyrite incrustations on the sheath's surface have been observed.

Dimensions. The mineralized three-dimensional sheaths have a diameter of 4-10 μm, the helix - 19-47 μm. In organic-walled forms, the mean width of the flattened sheath is 10-11 μm, which corresponds to the diameter of an unflattened filament of 7-8 μm. In one specimen, the width of the sheath varies, on the average from 1.2-1.3 times; its mean values in 26 measured specimens vary from 7.6 to 14.8 μm, the extreme variations from 6.6 to 16.3 μm. The lengths of the filamentous sheath range from 0.8 to 2.2 mm, most often 1.5-2 mm. The mean diameter of the helix is 50-60 μm, which is, approximately, 1.2-1.5 times as much as the living form. In one specimen, the helix diameter varies not more than 1.5 times, and usually is almost constant. In the 26 measured specimens, the mean values of the helix diameters vary from 38 to 84 μm, the extreme values from 35-102 μm. Figure 3*a* shows the distribution of values of the sheath width and helix diameter (variations of parameters shown for each measured specimen). Figures 3*b* and 3*c* are histograms showing the distribution of the number of measured specimens by the mean values of the sheath width and the helix diameter, correspondingly.

Comparison. *O. parva* differs from *O. pusilla* Golovenok, 1983, *O. blandita* Shenfil, 1980, *O. condensata* Liu, 1984, *O. minor* Zhang, 1984 and *O. parvissima* Song, 1984, in the larger diameters of both the filaments (sheath) and the helix (fig. 1); from *O. parvissima* also in the shape of cells in the trichome. It differs from *O. delicata* Reitlinger, 1948, in the smaller diameter both of the filament (sheath) (fig. 2) and of the helix, as well as by the fact that forms with a calcified sheath are not known. *O. parva* differs from other species of the genus in the smaller diameter of the filament and the helix (fig. 1).

Occurrence. Upper Vendian of the Siberian Platform (Tinnaya Formation of the Nokhtuysk section, the Lena River) and the East European Platform (beds with *Striatella coricea* Ass. and *Volyniella valdaica* Ass.; Zinkovo beds of the Yaryshevka Formation in Podolia; the Rozniche Formation of Volhynia; and the Upper Vendian of Finland from where the species has been described as *Volyniella cylindrica* Tynni et Donner, 1980), Ediacarian? of Saudi Arabia (Jubaylah Group), and Lower Cambrian of the Lesser Karatau (Chulaktau Formation) and


Filament Diameter (mkm)
25
20
15
10
5
1
10
30
50
70
90
110
130
Helix Diameter (mkm)
Obruchevella
delicata Reitl.
Obruchevella
parva Reitl.

Yunnan, China (the Meishucun or Yuhucun Formation), and North Greenland (the Portfjeld Formation).

Materials. Volhynia, Borehole No. 1547 (depth of 141-142 m), Rozniche Formation - several hundred specimens, of which 26 have been photographed and measured.

Volyniella Group

Volyniella Assejeva, 1974 emend. nov.

Volyniella: Assejeva, 1974, pp. 95-96 (part.); Kolosov, 1984, p. 53 (part.); non Paskeviciene, 1980, p. 48.

Obruchevella: Jankauskas et al., 1989, pp. 112-113 (part.).

Type species. *Volyniella valdaica* Assejeva, 1974.

Diagnosis. Organic-walled filamentous envelopes (width of envelope, when flattened, from 2.5 to 48 μm), hollow, without internal structures, terminally closed, thin, smooth, wrinkled, or with a transverse striation. Terminations of filament not tapering, rounded. Cellular structure unknown, noncellular (siphonal) structure possible. Filament coiled in cylindrical helix (when

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Fig. 2. Variation of *Obruchevella parva* Reitlinger, 1959, and *O. delicata* Reitlinger, 1948, as a function of helix and filament diameter. Horizontal and vertical bars denote range in size. Original dimensions of organic-walled microfossils before flattening are indicated by arrow. List of species and measured collections: 1-17 - *O. parva*: 1 - *O. parva*[1] (Reitlinger, 1959); 2 - *O. parva*[1] (Golovenok and Belova, 1983); 3 - *O. parva*[1] (Ogurtsova and Sergeev, 1987; Sergeev, 1992); 4 - *O. parva*[1] (Cloud et al., 1979); 5 - *O. parva*[1] (Kolosov, 1977); 6 - *O. parva*[1] (Yakshin and Luchinina, 1981); 7 - *O. delicata*[1] (Ogurtsova and Sergeev, 1987; Sergeev, 1992); 8 - *O.* cf. *O. parva*[3] Peel, 1988); 9 - *O. parva*[1] (Song, 1984); 10 - *O. parva*[1] (Wang et al., 1983); 11 - *Volyniella cylindrica*[4] (Tynni and Donner, 1980); 12 - *O. parva*[4] (Volhynian collection); 13 - *O. parva*[1] (Luo et al., 1984); 14 - *O. parva*[1] (Knoll and Ohta, 1988); 15 - *O. parva*[1] (reexamined type collection; Golovenok and Belova, 1989); 16 - *O. parva*[1] (Golovenok and Belova, 1989); 17 - *O. parva*[2] (Gorodnichev and Drobkova, 1991); 18-36 - *O. delicata*: 18 - *O. delicata*[2] (Reitlinger, 1948, 1959); 19 - *O. delicata* var. *elongata*[2] (Reitlinger, 1948, 1959); 20 - *O. delicata*[2] (Yakshin and Luchinina, 1981); 21 - *O. delicata*[2] (Shenfil, 1983); 22 - *O. delicata* f. *semeikini*[2] (Shenfil, 1983); 23 - *O. delicata*[2] (Drozdova, 1980); 24 - *O. delicata*[2] (Luchinina, 1975); 25 - *O. delicata*[1] (Song, 1984); 26 - *O.* aff. *O. delicata*[2] (Vologdin, 1958); 27 - *Lukaschevella spiralis*[2] (Vologdin, 1958); 28 - *L. tanuolaica*[2] (Vologdin, 1958); 29 - *Kordeella campylodroma*[2] (Vologdin, 1958); 30 - *Obruchevella sibirica*[2] (Reitlinger, 1959); 31 - *O. delicata*[3] (Bengtson et al., 1990); 32 - *O. delicata*[2] (Chuvashov et al., 1985); 33 - *O. delicata*[2] (reexamined type collection; Golovenok and Belova, 1989); 34 - *O. delicata* var. *elongata*[2] (reexamined type collection; Golovenok and Belova, 1989); 35 - *O. delicata*[1] (Golovenok and Belova, 1989); 36 - *O. delicata*[1] (Mankiewicz, 1992). Legend: [1] - silicified microfossils; [2] - calcareous algae; [3] - phosphatic remains; [4] - organic-walled microfossils.

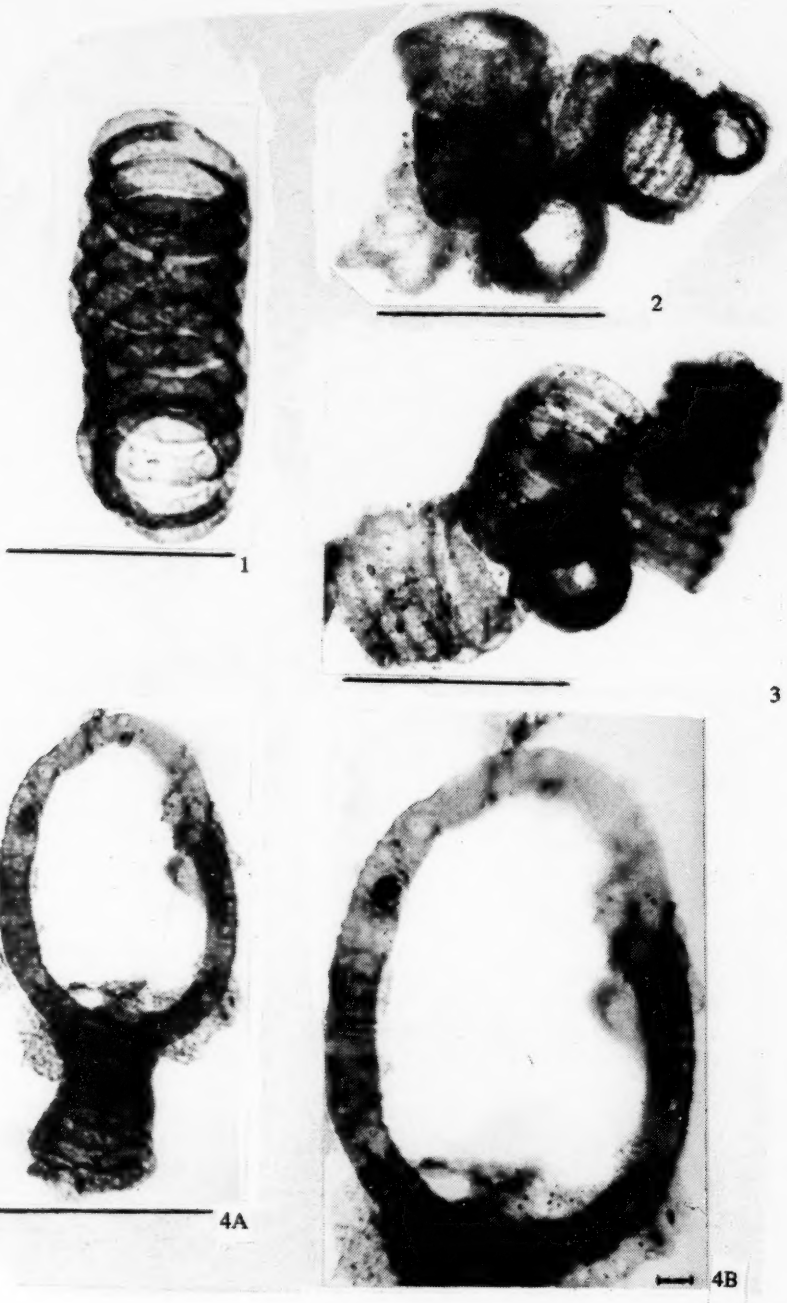


PLATE I

flattened, helix diameter from 18 to 360 μm), isodiametric or with a decreasing diameter toward terminations. Coils of helix not connected with each other, possibly touching or arranged freely; helix pitch equal to diameter of filament or slightly wider. Number of helix coils not exceeding 7, helix length not exceeding its diameter.

Species composition. Four species have been described, but there are, apparently, two more (fig. 4); one has not been described, and the second is misidentified as *V. valdaica*. The oldest and smallest (envelope width is 2.6-3.3 μm, helix diameter is 25-31 μm) member of the genus, from the Upper Riphean of the Miroyedikha Formation, Turukhansk region, Siberia, is depicted by Hermann as a "ringlike rolled filament of *Leiotrichoides*" (1990, table VIII, fig. 1). The next larger form (filament width 3-10 μm, helix diameter 18-72 μm) was first identified by Shepeleva as *Dictiosphaeridium*? sp. (Shepeleva, 1974); the same form was *Volyniella valdaica* Shepeleva (nom. nud.) (Shepeleva, 1973). Assejeva also included the description of *V. valdaica* Assejeva, small forms analogous to those described previously by Shepeleva that sharply differ from the holotype. The same form was referred to *V. valdaica* Ass. by Volkova (1985), Ragozina (1984), and Ragozina and Sivertseva (1985). All these described fossils show accurate dimensional characteristics of this form which need describing. The form is known from the Yartsevo (Borehole Yartsevo) and Redkino (Borehole Pereslavl'-Zalesskiy, Rostov, Nelidovo) formations and, possibly, the Povarovka Formation (Shepeleva, 1973, 1974) of the Moscow syneclise, the Yampol beds of the Mogilev Formation, and the Yaryshevka Formation of Podolia, the Chartory and Rozniche formations of Volhynia, the Lyamtsa, Arkhangelsk, Syuzma, and Zimniye Gory beds of the Ust'-Pinega Formation, and the Yerga beds of the Mezen Formation of the Arkhangelsk region.

V. jampolica Assejeva, 1974, has similar dimensions (filament width is 5-8 μm, helix diameter is 30-70 μm); it is from the Yampol beds of the Mogilev Formation in Podolia, and is characterized by transverse striation of the sheath. The specimen assigned to the same species by Hermann (1985, table XXIV, fig. 5) has striation different than the holotype; a similar form, however, is shown by Pyatiletov (1986, table V, fig. 5) from the Vanavara Formation of the Katanga Saddle (Siberian Platform).

KEY TO PLATE I

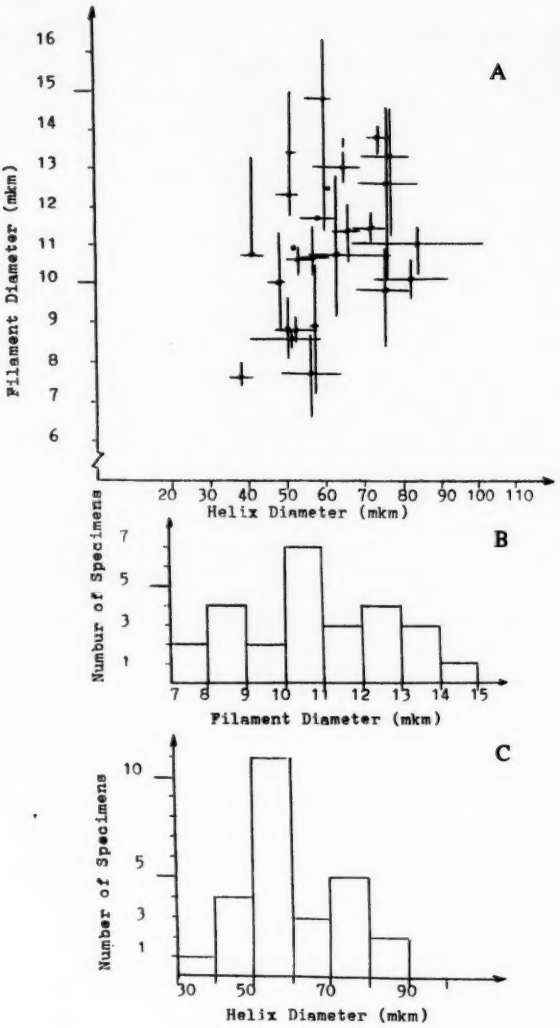
Fig. 1. PIN, Slide No. 4328a/11-14-1, sample 4. Solitary helicoid filament of *Obruchevella parva* Reitl., tubular structure of sheath well distinguished.

Fig. 2. PIN, Slide No. 4328a/11-14-1, sample 1. Cluster of *O. parva*.

Fig. 3. PIN, Slide No. 4328a/11-14-1, sample 2. Cluster of several samples of *O. parva*, showing, possibly, the natural positions of helicoid filaments in mat-like colonies. Differently oriented samples were deformed with different degree and different orientation.

Figs. 4*A*, *B*. *A* - PIN, Slide No. 4328a/11-14-1, samples 6 and 7. This specimen of *Boruokia* sp. (sample 6) was flattened together with specimen of *O. parva* (sample 7); *B* - *Boruokia* sp. (sample 6) is ringlike part of helicoid trichome with well-distinguished cells.

Samples are from Volhynia, Ukraine, Borehole No. 1547, depth 141-142 m, Slide No. 4328a/11-14-1; Upper Vendian, Rozniche Formation. Scale bar = 100 μm for 1-3, 4*A* and 10 μm for 4*B*.


A
Filament Diameter (mkm)
16
15
14
13
12
11
10
9
8
7
6
20 30 40 50 60 70 80 90 100 110
Helix Diameter (mkm)
B
Number of Specimens
7
5
3
1
7 8 9 10 11 12 13 14 15
Filament Diameter (mkm)
C
Number of Specimens
10
5
3
1
30 50 70 90
Helix Diameter (mkm)

The type species *V. valdaica* Ass. (filament width 9.2-22.4 μm, helix diameter 46-160 μm) is known from the Yaryshevka Formation of Podolia, the Rozniche Formation of Volhynia, the Staraya Russa Formation of the Leningrad region, the Syuzma and Zimniye Gory beds of the Ust'-Pinega Formation, and the Yerga beds of the Mezen Formation in the Arkhangelsk region. The largest sizes are the following species: *V. torta* Kolosov, 1984 (filament width 18-32 μm, helix diameter 160-280 μm) and *V. rotundata* Kolosov, 1984 (filament width 32-48 μm, helix diameter 13-360 μm) from the Kursov and Iktech formations of the Nepa-Botuoba region, West Yakutia. The following species are excluded from the genus: *V. inviolata* Kolosov, 1984 (assigned to *Obruchevella*); *V. concentrica* Kolosov, 1984 (generic affinity not clear); *V. glomerata* Jankauskas, 1980 (this species has different structure than the genus - it is a clew of several filaments); and also *V. canilovica* Asseyeva, 1974, *V. rara* Paskeviciene, 1980; *V. rudaminica* Pask., 1980; and *V. ignalinica* Pask., 1980 (assigned to *Cochleatina* Assejeva, 1983).

Comparison. *Volyniella* differs from the genus *Obruchevella* Reitlinger, 1948, emend. nov., in appearing to be an envelope closed at terminations, but not a sheath, and in that the helix coils are never connected. Therefore, when *Volyniella* is flattened, the helix usually has a disintegrated shape. Also, the length of the helix does not exceed its diameter. Differences in the mode of life are also possible: *Volyniella* is planktonic and *Obruchevella* benthonic. It differs from *Tubulosa* Assejeva, 1982, in closed terminations of the envelope, the thickness of the envelope, and in that the envelope is never crimped, and the helix is always cylindrical, not just two or three ringlike turns. *Volyniella* differs from *Boruokia* Kolosov, 1984, in the absence of septa and, probably, in the noncellular structure as well as in the coiling of the filament in a cylindrical helix, not just one or two ringlike turns. It differs from the *Spirillopsis* gen. nov. in its size, a considerably shorter helix, and in the absence of pyrite crystals inside the envelope. It differs from *Spirellus* Jiang in Luo et al., 1982, in the size (of both the filament and the helix) and in the nature of preservation (*Volyniella* is known only as organic-walled, and *Spirellus* is phosphatized; a direct collation of different forms of preservation is premature). *Volyniella* differs from other genera with a spiral and ringlike shape (*Tortunema* Hermann, 1976, *Glomovertella* Reitlinger, 1958, *Jiangispirellus* Peel, 1988), as well as those with ringlike bent filaments, in the closed envelope, in the absence of cellular structure, and in the cylindrical shape of the helix.

Discussion. When genus *Volyniella* Assejeva, 1974 was first described, it included *V. canilovica* Assejeva, 1974, which had an altogether different structure (a concentric chitinoid helix with an intricate morphogenesis). Later Paskeviciene described three more species with a similar exotic structure. In 1983, Assejeva erected a new genus *Cochleatina* Assejeva, 1983, and included in it *V. canilovica*, *V. rara*, and *V. ignalinica*; she first referred *V. rudaminica* to the genus *Cochleatina* only in 1989, in explanations to plates in the monograph "Precambrian Microfossils of the USSR." In 1984, Kolosov was the first to show closed terminations of the filamentous envelope as a diagnostic feature of the genus *Volyniella*; he also recognized as generic characters the changeable width of the envelope and irregularity of the cylindrical helix. These are rather indirect characters and are connected with peculiar deformations of short helices, in which coils

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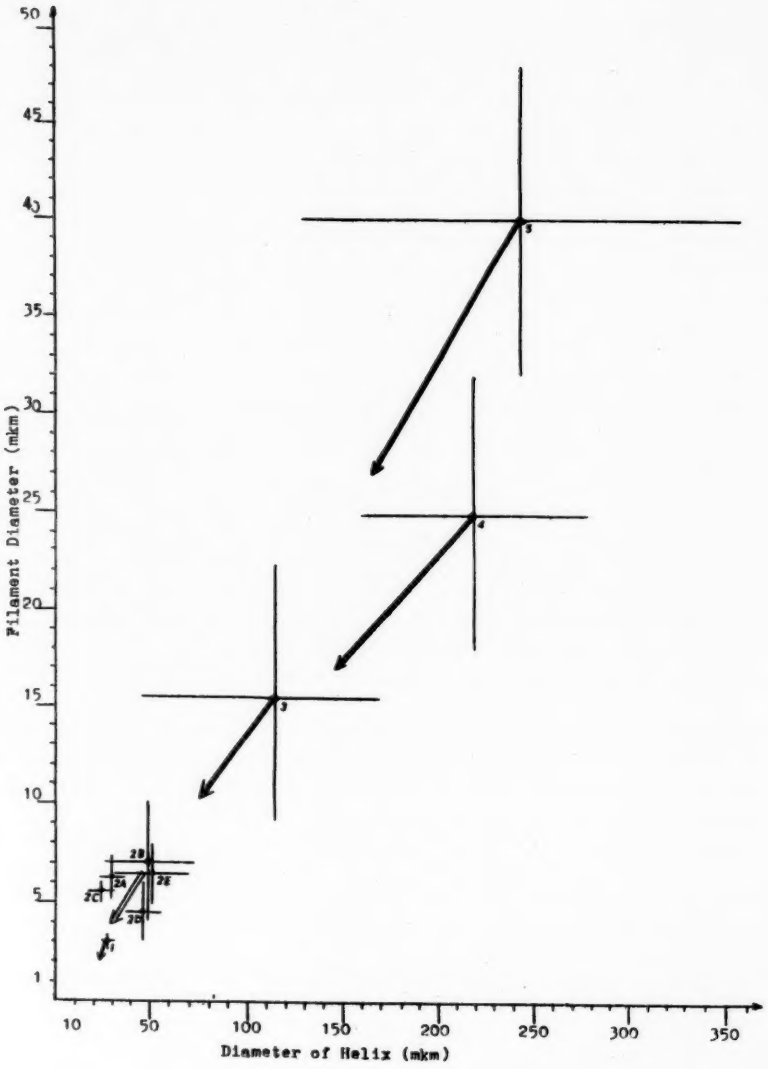
Fig. 3. *Obruchevella parva* Reitl. from Volhynian collection of organic-walled microfossils. A - variation of specimens as function of helix and filament diameter. Horizontal and vertical bars denote range in size. B, C - size of distribution of measured specimens: B - filament diameter, C - helix diameter.


Filament Diameter (mkm)
50
45
40
35
30
25
20
15
10
5
1
10
50
100
150
200
250
300
350
Diameter of Helix (mkm)
5
4
3
2D
2A
2E
2C
2B

are not connected and do not characterize living features. I cannot agree that the *Volyniella* filament might be segmented, because true septa are not discernible in any specimens; the apparent segmentation is rather a striation of the envelope which, of course, may represent traces of the cells, but that has not yet been proved. In the monograph "Precambrian Microfossils of the USSR" (1989), *Volyniella* is considered as a junior synonym of *Obruchevella*, and two species of *Volyniella* are assigned to other genera. I cannot agree with this assignment of species among several genera. It is exactly for this reason that the genus *Volyniella* Assejeva, 1974, is being restored.

Volyniella valdaica Assejeva, 1974, emend. nov.

Pl. II, figs. 1-5; Pl. III, fig. 2

non *Volyniella valdaica* Shepeleva (nom. nud.): Shepeleva, 1973, pp. 13-14 (=*Dictiosphaeridium*? sp., Shepeleva, 1974, pl. IV, figs. 4, 10).

Volyniella valdaica: Assejeva, 1974, p. 96 (part.), pl. fig. 1, non figs. 2, 3; 1976, pl. XVIII, fig. 1, non figs. 3-5; 1983, pl. VI, fig. 12, non fig. 11; Assejeva in Velikanov et al., 1983, pl. XVII, figs. 10, 11, non pl. XII, fig. 4; Assejeva in Volkova, 1985, pl. LVI, fig. 4, non fig. 5; Hermann, 1985, p. 148, pl. LXXIV, figs. 3, 6, 7.

non *Volyniella valdaica* Assejeva: Ragosina, 1984, pl. I, fig. 8; Ragosina and Sivertseva, 1985, pl. LVIII, figs. 22, 23; Pyatiletov, 1986, pl. V, fig. 5.

Obruchevella valdaica: Jankauskas et al., 1989, p. 115, pl. L, figs. 1, 2.

Leiotrichoides sp.: Ragosina and Sivertseva, 1985, pl. LX, fig. 9.

Spiromorpha sp.: Timofeev, 1973, pl. II, fig. 10, pl. XIV, figs. 7-9; non pl. XII, fig. 2.

Holotype. Institute of Geological Sciences, Ukrainian Academy of Sciences, slide 82, sample 242/1; Podolia, Gusjatin village, Borehole No. 11673, depth 574 m; Upper Vendian, Yaryschev Formation, Zinkovo Beds (Assejeva, 1974, p. 96, pl., fig. 1).

Description. Filamentous envelopes are hollow, with closed terminations, thin (envelope's width is much less than 1 μm), smooth, without signs of an internal cellular structure and of

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Fig. 4. Variation of *Volyniella* as a function of helix and filament diameter. Horizontal and vertical bars denote range in size. Original size before flattening is indicated by arrow. List of species: 1 - *V.* sp. - ringlike coiled filament of *Leiotrichoides* (Hermann, 1990); 2 - *V.* sp.: 2*A* - "*V. valdaica*" (Pyatiletov, 1986, pl. V, fig. 5); 2*B* - "*V. valdaica*" (Shepeleva, 1974, pl. IV, figs. 4, 10); 2*C* - "*V. valdaica*" (Assejeva, 1976, pl. XVIII, fig. 5; Velikanov et al., 1983, pl. XII, fig. 4); 2*D* - "*V. valdaica*" (Ragozina and Sivertseva, 1985, pl. LVIII, figs. 22, 23) + "*V. valdaica*" (Ragozina, 1984, pl. I, fig. 8) + *V.* sp. (Ragozina, 1984, pl. I, fig. 9); 2*E* - *V. jampolica* (Assejeva, 1974); 3 - *V. valdaica* (Volhynian collection + specimens indicated in synonymica); 4 - *V. torta* (Kolosov, 1984); 5 - *V. rotundata* (Kolosov, 1984).

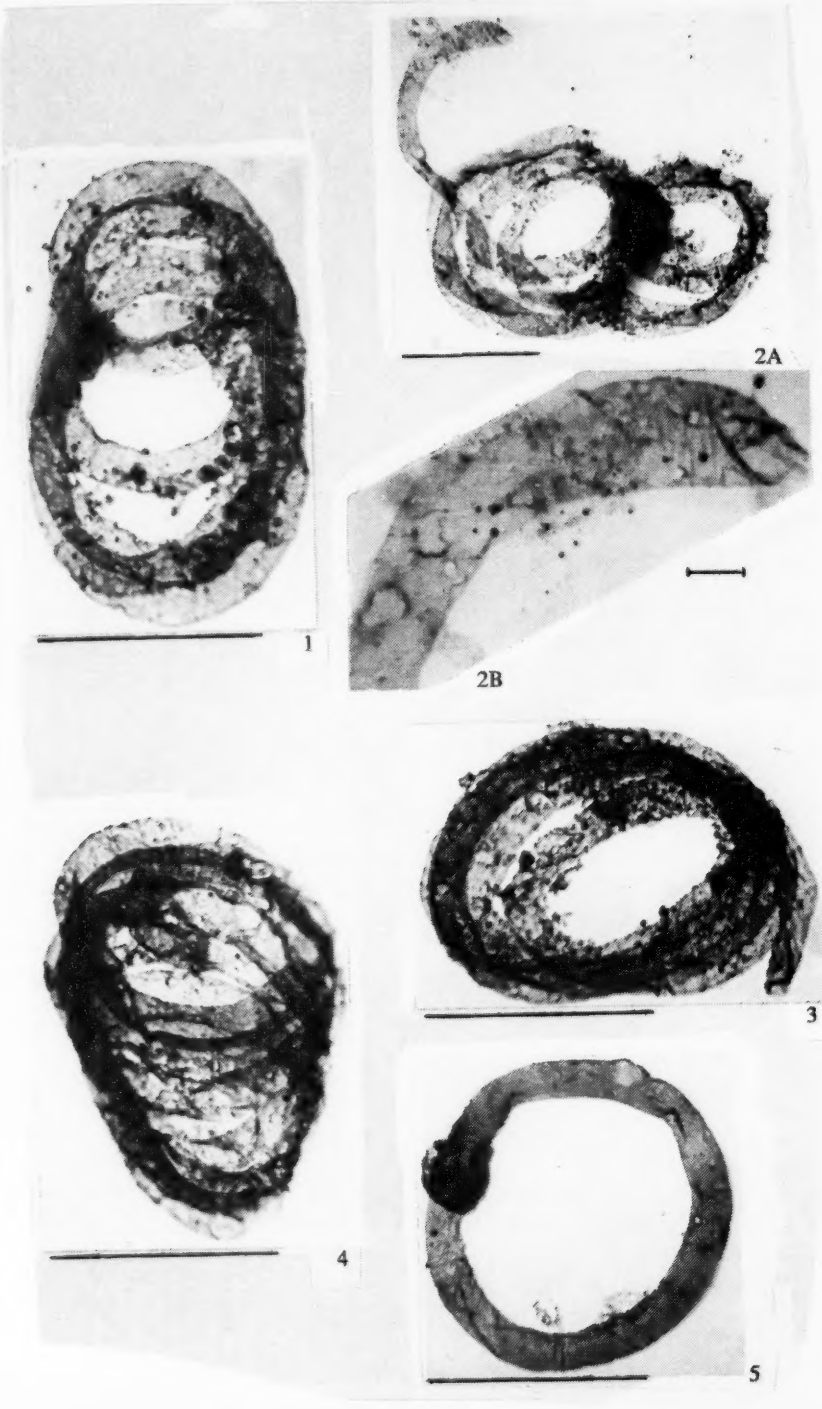

PLATE II

constant width. I have failed to observe both terminations of the filament in any specimens; however, in several specimens, one termination is preserved and is rounded, not tapering. The filament is coiled in a regular cylindrical helix, which during life was evidently isodiametric. The helix coils are not connected, may touch, or are arranged freely; the helix pitch during life was a little more than the filament diameter. The number of helix coils is from 1 to 6, average of 4. Annular fragments occur where, at the place of joining or overlapping of filament terminations, is a thickening or a round body obscuring the filaments and producing the impression of a closed ring (pl. II, fig. 5).

Preservation. Flattening of the fossils during lithification has resulted in an envelope wider than the filament diameter by almost 1.5 times, and in a distortion of the shape of the helix coil and the helix itself. Since the helix coils were not connected, the helix as a whole was not deformed, and its coils were shifted in relation to one another, and flattened almost always in the direction perpendicular to the axis of coiling of the helix; therefore, the diameter of coils was distorted only because of shifting coils, not because of flattening. Such distortions may be recognized by a deformation of the filament envelope in all cases, as soon as the radius of its curvature changes as compared to the original one. In several specimens are tiny annular wrinkles near the filament's termination, and in one specimen, annular folds are arranged along the filament, which look like annular bulges of the envelope (length of bulges is from 0.9 to 1.4 μm; distance between bulges, in one site, is from 1.1, to 11 μm). Usually the envelopes are hollow, light yellow and transparent, but some specimens are darker, due to organic matter preserved inside the envelope. In these cases, spots of a darker color, sometimes divided by lumens, or almost the entire envelope filled with a dark matter are seen. Such spots imitate a cellular structure but I have failed to observe clearly defined septa. At the termination of the filament is often an oval deformation, outlined by folds of the envelope; the very termination of the filament is sometimes torn off. In the uncoiling of the helix (probably postmortem, but occurring apparently before its flattening), the filament is not stretched straight, but becomes cuspate, consisting of segments of a circle, in whose joints the filament is pressed, bent or twisted along. I suggest that the fragmentation into rings occurred during life, and was probably connected with reproduction, but I have no evidence for that. In the helix fragments of 1.5-2 coils, the filament terminations are torn off, suggesting that this fragmentation reflects only the degree of preservation. Helices of 4 coils and more preserve, as a rule, one of the filament terminations, that is, such specimens demonstrate the full size of the helix and filament. Framboidal pyrite aggregrates incrusting the envelope's surface are found in several specimens.

Dimensions. The mean width of a flattened envelope is 15-16 μm, which corresponds to

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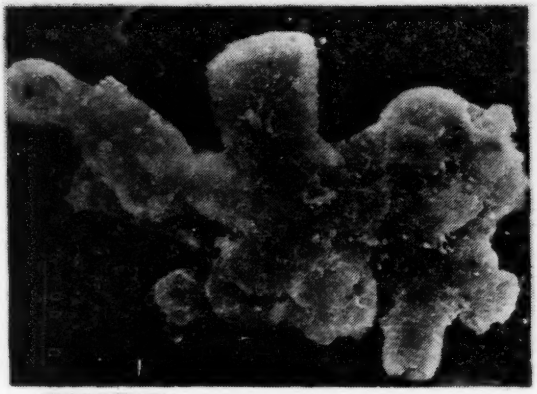
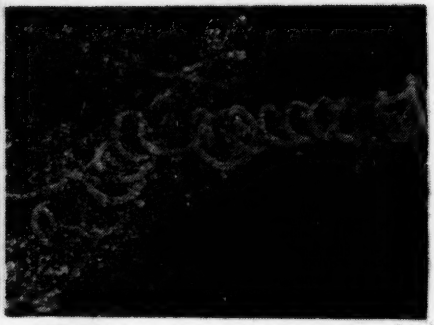
KEY TO PLATE II

Figs. 1-5. *Volyniella valdaica* Ass.; Volhynia, Ukraine, Borehole No. 1547, depth 129-132 m, Slide No. 4328a/11-13-3; Upper Vendian, Rozniche Formation: Fig. 1 - PIN, Slide No 4328a/11-13-3, sample 5, Fig. 3 - sample 16, Fig. 4 - sample 14. These specimens have different degrees of recoiling and distortion. Fig. 2A, B - PIN, Slide No. 4328a/11-13-3, sample 6. This sample has closed terminations. Fig. 5 - PIN, Slide No. 4328a/11-13-3, sample 3. The ringlike fragments of helix with dark body on the place of overlapping of filament termination may be hormogonium-like structure. Scale bar = 100 μm for 1, 2A, 3-5, and 10 μm for 2B.

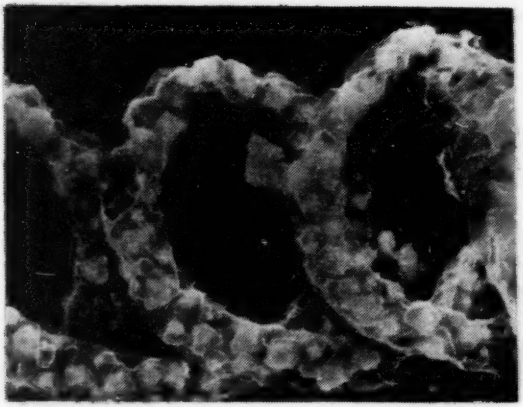


1

2



3A



3B

PLATE III

the diameter of an unflattened filament of about 10 μm. The filament widths (in one specimen) may vary, on the average, 1.5 times; the mean widths of filaments in 23 measured specimens vary from 11.8 to 19 μm; extreme values of the variations are from 9.2 to 22.4 μm. In complete specimens the filament length reaches 1.5-2 mm. The mean helix diameter is 110-120 μm; however, the helix diameter during life was probably, on the average, 90-100 μm, taking into account shifts of coils and the degree of preservation. The helix diameter varies on the average, 1.5 times, but may also vary 4 times. In the 23 measured specimens, the mean values of helix diameters vary from 86 to 135 μm, and extreme values of the variations are from 46 to 170 μm. In fig. 5*A*, is the distribution of mean values of the filament width and the helix diameter, and variation limits for these parameters in each of the measured specimens. In figs. 5*B* and 5*C* are histograms showing the distribution of the number of measured specimens according to values of the filament width and the helix diameter, correspondingly.

Comparison. *Volyniella valdaica* differs from other species of the genus in its dimensions: from small species by larger values of both the envelope diameter (width) and the helix diameter; from *V. torta* Kolosov, 1984, and *V. rotundata* Kolosov, 1984, in the narrower envelope width and helix diameter, as well as in the smooth envelope without a striation.

Occurrence. Upper Vendian, Redkino Horizon, beds with *Striatella coriacea* Ass. and *Volyniella valdaica* Ass. of the East European Platform; the Yaryshev Formation of Podolia, the Rozniche Formation of Volhynia, the Staraya Russa Formation of the Leningrad region, the Syuzma and Zimniye Gory beds of the Ust'-Pinega Formation, and the Yerga beds of the Mezen Formation, Arkhangelsk region.

Material. Volhynia, Borehole No. 1547, depth of 122 m, 129-132 m and 142-143 m, Rozniche Formation - 83 specimens, 23 photographed and measured; Leningrad region, Borehole C-270 CGA "Sevzapgeologiya," depth 98-98.5 m, Staraya Russa Formation - 4 specimens.

Spirillopsis Group

Spirillopsis Burzin, gen. nov.

Specific name. From *spirillum* (Latin, tiny spiral) and *opsis* (Greek, image).

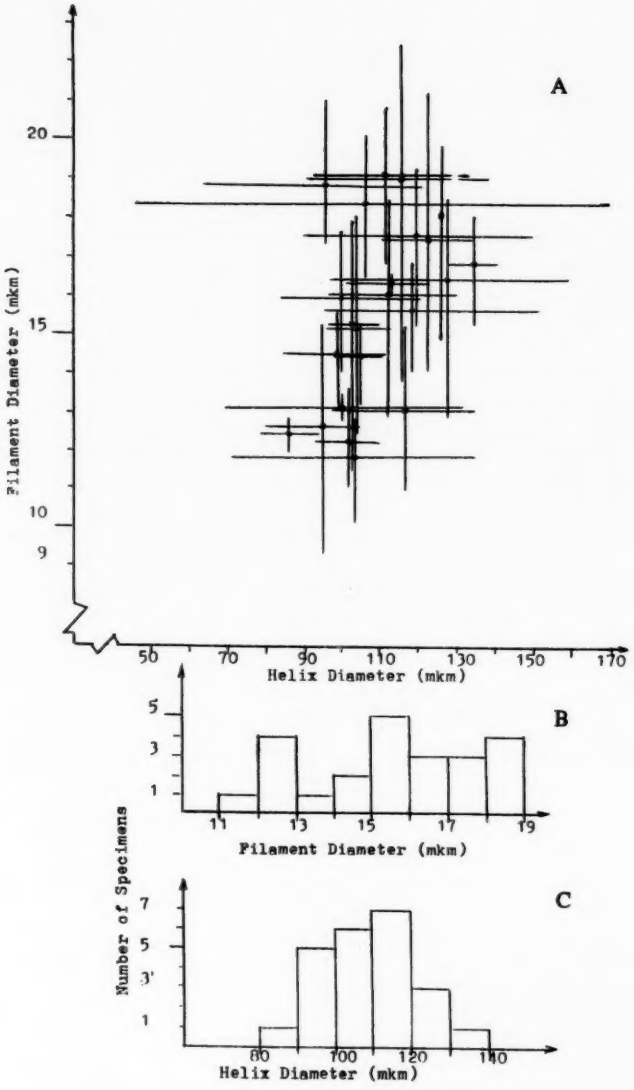
KEY TO PLATE III

Fig. 1. Cluster of *Obruchevella parva* Reitl.; helix coils closely touching and forming solid "tube" of coils; Borehole No. 1547, depth 141-142 m, SEM table No. 4, sample 5.

Fig. 2. *Volyniella valdaica* Ass.; helix stretched, coils do not touch one another; depth 141-142 m, SEM table No. 4, sample 2.

Fig. 3A, B - *Spirillopsis pyritofera* Burzin, gen. et sp. nov.: A - general view of helix, B - some coils of helix, smooth tubular sheath and pyrite crystals inside it; depth 117.5-118.5 m, SEM table No. 4, sample 6.

All samples from Volhynia, Ukraine, Borehole No. 1547; Upper Vendian, Rozniche Formation. Microphotographs by SEM Jeol Superprobe 733. Scale bar = 100 μm for 1, 2, 3A, and 10 μm for 3B.


A
20
15
10
9
Filament Diameter (mkm)
50
70
90
110
130
150
170
Helix Diameter (mkm)
B
5
3
1
11
13
15
17
19
Filament Diameter (mkm)
C
Number of Specimens
7
5
3
1
80
100
120
140
Helix Diameter (mkm)

Type species. *Spirillopsis pyritofera* Burzin, sp. nov.

Diagnosis. Filamentous thin-walled tubular organic sheaths 1.4-11 μm wide, with pyrite crystals inside (crystal size from 1 to 5 μm). Pyrite crystals arranged singly, regularly along filament or in clusters filling entire inner space of sheath. Terminations of sheath not known. Filament coiled in helix—from cylindrical isodiametric to flat concentric, with diameter of 29-143 μm (when flattened). Helix turns arranged freely, in cylindrical forms helix length exceeding diameter many times. Number of turns possibly, up to 40.

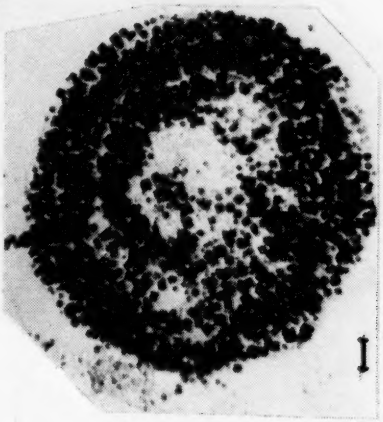
Discussion. This genus is known only as an organic-walled form, or to be more precise, as a combination of an organic-walled sheath and mineral inclusions. Like *Zinkovioides* Hermann, 1985, three interpretations of these fossils are possible (Burzin, 1993): (1) This represents an unusual form of preservation of morphological analogs of cyanobacteria, associated with the formation of pyrite pseudomorphs during the decaying of cytoplasm. This could have been possible in the basin sea at the end of Redkino Time, but impossible in Kotlin Time, when there were grounds to assume desalinated conditions. (2) This represents a different form of preservation of cyanobacteria, also connected with the formation of pyrite pseudomorphs during the decaying of organic matter, but induced not only by burial in the sea; burial was in hydrogen sulfide pollution of the sediment. (3) This does not represent a special form of preservation of cyanobacteria, but an altogether different group of organisms analogous to recent Beggiatoaceae. The pyrite formation was connected with living hydrogen sulfide environments, and the presence of sulphur granules in cells have initiated a postmortem formation of pyrite crystals in each cell. Of these three interpretations, the first is most unlikely, because, if we accept it, we would expect a vast majority of Precambrian microbiotas, including those in cherts, to exist in nonmarine conditions, and this is improbable. The third interpretation is most probable, because in the same beds with *Spirillopsis* and *Zinkovioides* are the remains of apparent plankton and most of the filamentous forms contain pyrite crystals, not inside the sheaths or envelopes, but as a surficial incrustation. This substantiates the existence of hydrogen sulfide pollution and also provides evidence for a special form of preservation reflecting biological differences. All this provides the basis for considering this form as a representative of sulphuric filamentous bacteria.

Species composition. Type species.

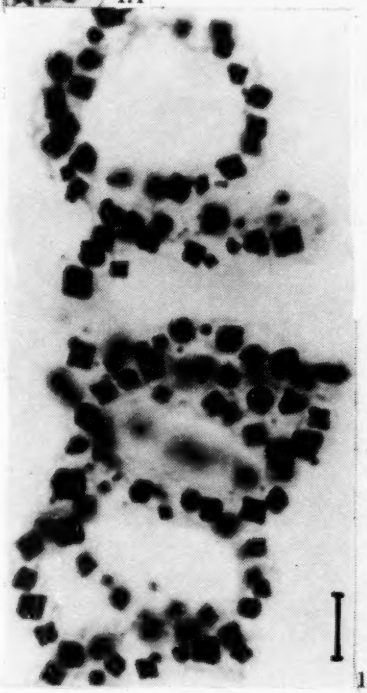
Comparison. *Spirillopsis* differs from all genera with a helix structure in the presence of pyrite crystals inside the sheath. It differs from *Zinkovioides* Hermann, 1985, in the filamentous envelope coiled in a helix. From *Nostocomorpha* Sin et Liu, 1978, it differs in the filament having an organic sheath and being coiled in a regular helix. It differs from *Ferrimonilis* J. Oehler, 1977, in its larger size (the filament's width and length, and pyrite crystal sizes), and in a filament coiled in a regular helix.

Fig. 5. *Volyniella valdaica* Assejeva from Volhynian collection of organic-walled microfossils. A - variation of specimens as function of helix and filament diameter. Horizontal and vertical bars denote range of size. B, C - size distribution of measured specimens: B - filament diameter, C - helix diameter.

1A



2



1B

1C

PLATE IV

Spirillopsis pyritofera Burzin, sp. nov.

Pl. III, fig. 3A, B; Pl. IV, figs. 1-2; Pl. V, figs. 1-4

Spiral-like filamentous microfossils: Burzin, 1993, pl. I, fig. 7.

Etymology. From the mineral, pyrite, and *fero* (Latin - to bear).

Holotype. PIN, Slide No. 4328a/11-11-1, Specimen 3; Volhynia, Borehole No. 1547, depth of 117.5-118.5 m, Rozniche Formation; Upper Vendian, Redkino Horizon, beds with *Striatella coriacea* Ass. and *Volyniella valdaica* Ass.

Description. Sheath is tubular, thin-walled (thickness much less than 1 μm), smooth, transparent, of a constant width, and without any cellular structures inside. Sheath terminations are not known. Cubic, octahedral, and similar pyrite crystals of 1-5 μm are inside the sheath. The crystals are arranged either singly (small and large) in a chain (mean distance between crystals is 1-3 μm), or by clusters (only tiny crystals) when a mass of crystals fills the entire sheath's volume. The filament is coiled in a helix which, evidently, was regular, cylindrical, and isodiametric during life; the helix turns are arranged closely, the helix pitch being always larger than the sheath's diameter. The helix did not have a rigid shape, and could be easily deformed; turns are uncoiled, up to a flat concentric helix. The number of helix coils is from 3 to more than 39, as a rule, more than 10. Probably during life, the helix length exceeded its diameter many times.

Preservation. Judging by the fact that pyrite crystals fill the interior of the sheath, that the sheath envelopes them tightly, and that the sheaths with no pyrite crystals inside are flattened, one may assume that pyrite crystal arrangement suggests that it may reflect a cellular structure of the filament. If this is the case, then the filament consisted of cells whose length (3-8 μm) was equal to their diameter. In some specimens, the helix is preserved in a regular cylindrical isodiametric shape. In most specimens, the helix shape is deformed to a greater or lesser degree: the coils are stretched, the axis of coiling of the helix is curved, some of the turns are incoiled with one coil overlapping another, and the helix changes from cylindrical to flat concentric. The sheath is flattened where there are no pyrite crystals, and its width exceeds almost 1.5 times the diameter during life. When one big crystal inside the sheath is present, the sheath envelops it from all sides, and its width is less than its diameter during life. It is probably only where the sheath is filled with small crystals that we can observe the size of the sheath which existed during

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KEY TO PLATE IV

Figs. 1, 2. *Spirillopsis pyritofera* Burzin, gen. et sp. nov.; Volhynia, Ukraine, Borehole No. 1547, depth 117.5-118.5 m, Slide No. 4328a/11-11-1; Upper Vendian, Rozniche Formation. Fig. 1 - PIN, Slide No. 4328a/11-11-1, sample 3, holotype: A - general view of helix; B, C - fragments of helix, thin tubular sheath and pyrite crystals regularly arranged are distinguished; Fig. 2 - PIN, Slide No. 4328/11-11-1, sample 8, flat spiral; it is possible that this sample was recoiled. Scale bar = 100 μm for 1A, 2, and 10 μm for 1B, C.

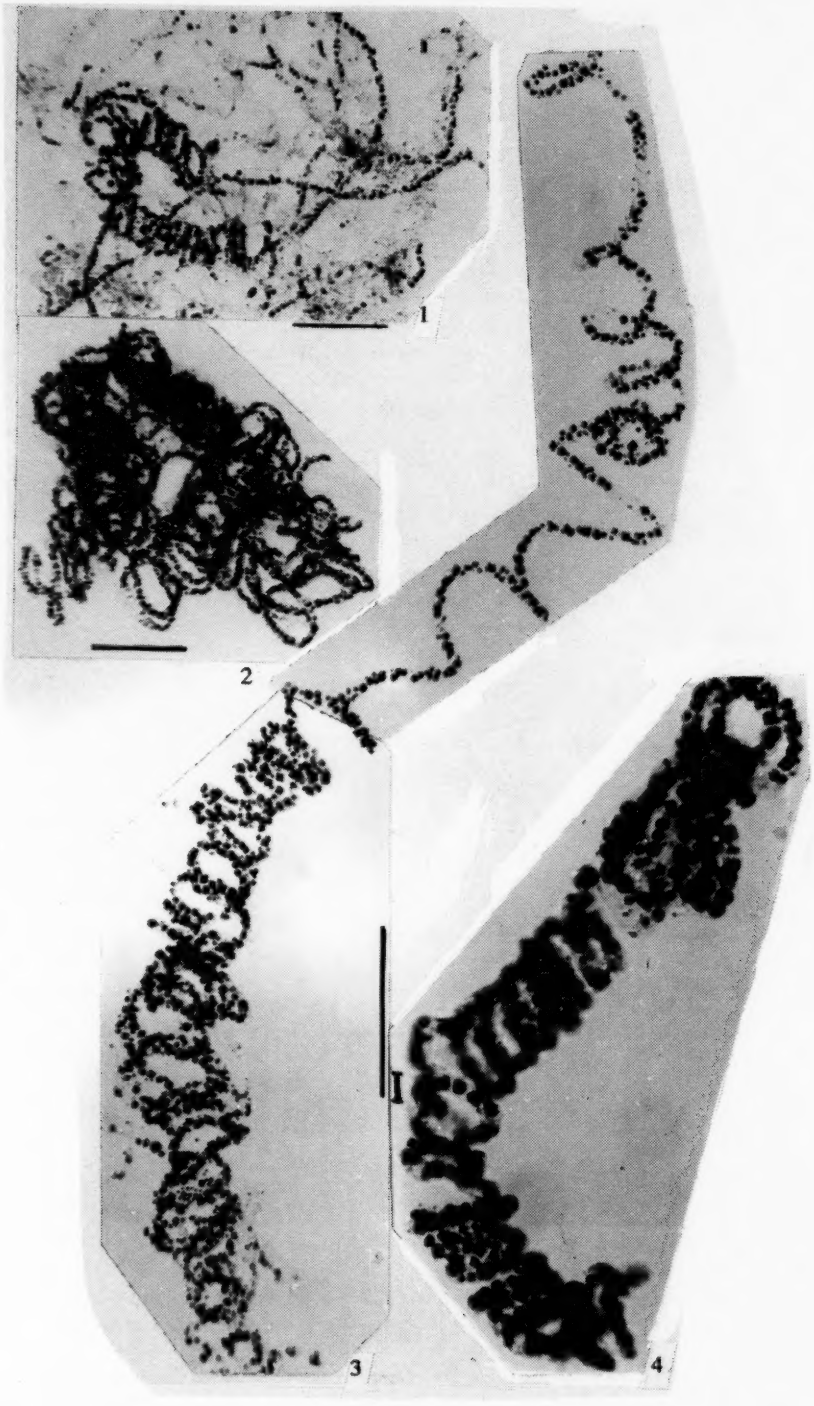

PLATE V

life. The helix coils are always flattened independently of each other; therefore, in specimens with a cylindrical helix, the diameter of a coil is 1.2-1.3 times larger as compared to that during life. Most often helices occur singly, often on mats of *Zinkovioides inclusis* Herm. filaments, but sometimes they occur in assemblages, and then the helices always have a regular cylindrical shape. It seems most probable that different shapes of helices are caused exactly by its postmortem deformations, not by differences in the filament's form of growth during life. It is in cylindrical helices that the regularity of the structure (that is, the best preservation) is observed; therefore, the specimen with the most solid, isodiametric and long helix, whose axis of coiling is only slightly curved, has been chosen as the holotype. Judging by the fact that the best degree of preservation of the helix is observed in assemblages, I assume the species to have been benthic, which is consistent with their comparison with recent Beggiatoaceae. There are no framboidal pyrite aggregates or pyrite incrustations on the surfaces of the sheaths.

Dimensions. The sheath width is, on the average, 5-6 μm, which probably corresponds almost to the diameter during life. In one specimen, the sheath width from one area to another varies 1.5-2 times (due to distortion both in flattening and in enveloping the crystals). In 11 measured specimens, the average values of the sheath widths vary from 2.9 to 9.3 μm; the extreme values of variations are 1.4-11 μm. In the measured specimens, the sheath length is from 0.6 to 4 mm. The mean diameter of the helix is 30-40 μm in regular cylindrical forms and 50-80 μm in uncoiled helices. The helix diameter during life was probably 25-30 μm. In cylindrical helices, the diameter of turns in one specimen varies 1.3-2.5 times; in flat concentric helices, the helix diameter varies, on the average, within the same range, but may also be wider. In 11 measured specimens, the mean values of the helix diameters vary from 35 to 118 μm; the marginal values of variations are 19-143 μm. Figure 6*A* shows the distribution of values of the sheath width and the helix diameter (variations of parameters are shown for each specimen); Figures 6*B* and 6*C* are histograms of the distribution of the number of specimens measured by the mean values of the sheath width and the helix diameter, correspondingly.

Discussion. The only form comparable with the described species is *Palaeolyngbya corticellata* Luo et Wang, 1982 (silicified microfossils), whose filament is a cylindrical helix; long opaque sites of the filament alternate with short transparent ones (Luo et al., 1984, pl. 1, fig. 5). This distribution resembles some specimens of my species, in which sites filled with pyrite crystal aggregates alternate with sites with no crystals inside the sheath. However, the authors of *Palaeolyngbya* do not indicate pyrite crystals inside, nor are crystals observed in the pictures.

Materials. Volhynia, Borehole No. 1547, depth 117.5-118.5, 119.5-120 m, 122 m, and 129-132 m, Rozniche Formation; 60 specimens, 13 photographed and 11 measured.

KEY TO PLATE V

Spirillopsis pyritofera Burzin, gen. et sp. nov.; Volhynia, Ukraine, Borehole No. 1547, depth 117.5-118.5 m, Slide No. 4328a/11-11-1; Upper Vendian, Rozniche Formation. Fig. 1 - PIN, Slide No. 4328a/11-11-1, sample 1, distorted helix on mat of filamentous sulphur bacteria *Zinkovioides inclusis* Herm.; Fig. 2 - PIN, Slide No. 4328/11-11-1, sample 14, cluster of some samples; Fig. 3 - PIN Slide No. 4328a/11-11-1, sample 11; Fig. 4 - sample 5, helices distorted and recorded with different degree. Scale bar = 100 μm.

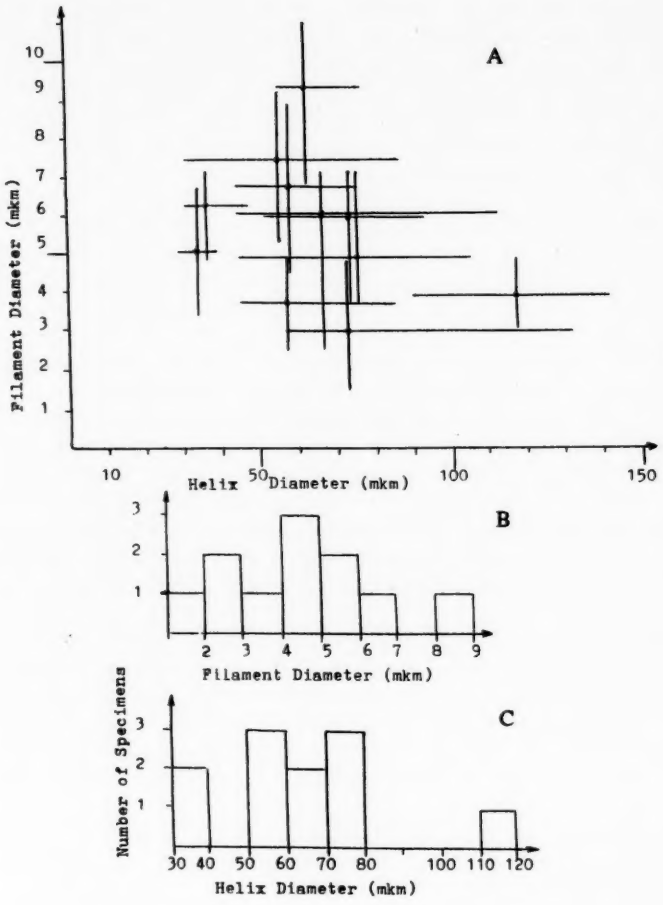

Fig. 6. *Spirillopsis pyritofera* Burzin, gen. et sp. nov. A - variation of specimens as function of helix and filament diameter. Horizontal and vertical bars denote range of size. B, C - size distribution of measured specimens: B - filament diameter, C - helix diameter.

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Moresnetia-LIKE PLANTS FROM THE UPPER DEVONIAN OF MINUSINSK BASIN, SIBERIA

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Abstract: Siberian plants previously assigned to *Moresnetia* are separated in a new genus *Lenlogia* with cupule-like clusters of paired and proximally fused sporangia. The latter feature distinguishes the new genus from *Protopteridophyton* Li et Hsu. Its relation to progymnosperms is discussed.

Сибирские растения, ранее относимые к *Moresnetia*, выделенные в новый род *Lenlogia*, принадлежащий группе девонских голосеменных, но отличающийся от других ее родов терминальным положением семяпочек на вторичных лопастях купул. Совместно найденные почковидные органы интерпретированы как двусемядальные проростки того же растения.

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In 1959 Ananiev [1] assigned dichotomous axes with distally clustered appendages from the Upper Devonian of Minusinsk Basin, Siberia, to *Moresnetia zalesskyi*, a species described by Stockmans from the stratigraphically equivalent beds in Belgium [9]. Stockmans has provided Ananiev with a few specimens from the original material for comparison with the Siberian fossils. These materials are now deposited in the Tomsk University Museum.

The putative *Moresnetia* axes from Siberia were accompanied by a reniform body reported as the first Devonian seed [2].

In 1986 Professor Ananiev courteously provided us with an opportunity to examine his specimens from Siberia and Belgium. Our impression was that they belonged to a plant of pteridophytic affinities.

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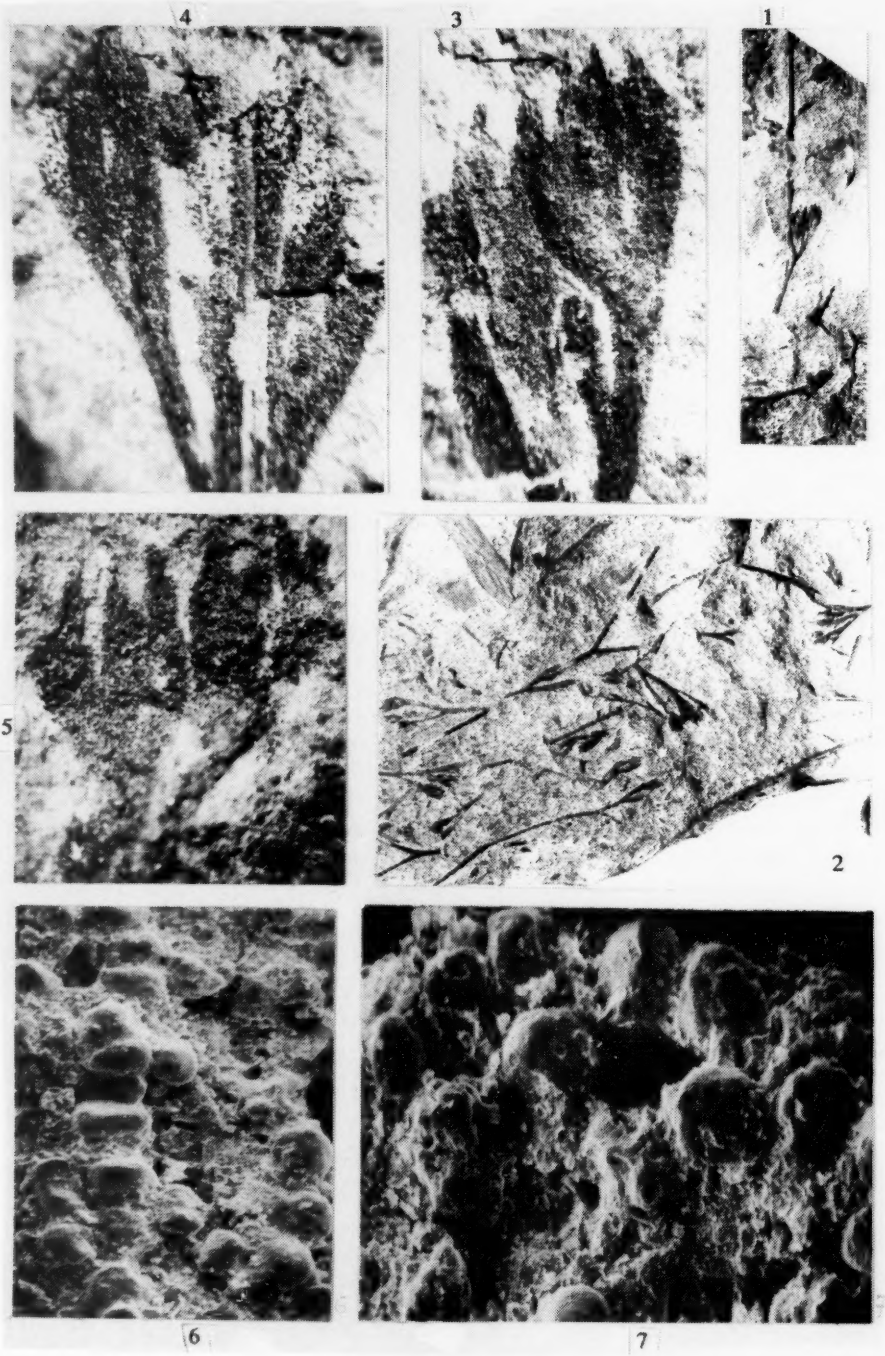

PLATE I

At the same time we thought the Siberian and Belgian fossils similar enough to be assigned to the same genus. Our paper was reviewed by S. E. Scheckler who informed us of then yet unpublished *Moresnetia* seeds [3]. These findings urged us to re-examine our material which eventually was assigned to a new genus.

Lenlogia Krassilov et Zakharova, gen. nov.

Name. After Lennyj Log, the type locality.

Type species. *Moresnetia kryshtofovichii* Radczenko in Petrosyan [7], Lennyj Log, Minusinsk Basin, Upper Devonian.

Diagnosis. Forked axes with protostele of scalariform and annular tracheids, bearing condensed clusters of sympodially branched appendages bearing terminal bisporangiate synangia. Sporangia erect, fused up to 2/3 their length. Spores of one kind, smooth, trilete.

Lenlogia kryshtofovichii (Radczenko) comb. nov.

Pl. I, figs. 1-7; Pl. II, figs. 1-4; Pl. III, fig. 5

Lectotype: No. 40-92, Tomsk University Museum, figured in [1] plate 18, fig. 1, [2], plate 7, fig. 1*a*.

Moresnetia zalesskyi: Ananiev, 1959 [1], p. 31, Pl. 18, fig. 1; Ananiev, 1963 [2], p. 340, Pl. 7, fig. 1*a*, *b*.

Moresnetia kryshtofovichii: Radczenko in Petrosyan, 1959 [7], p. 96, Pl. 1, figs. 1-3; Radczenko in Lepekhina et al., 1962 [5], p. 132, Pl. 20, figs. 1-6.

Diagnosis. As for the genus.

Description. Specimens 40-92, 40-94, 40-163 and 50-3 from Ananiev's collection are sandstone slabs covered with impressions and compressions of longitudinally striated dichot-

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KEY TO PLATE I

Fig. 1. *Lenlogia kryshtofovichii* - axis with a sporangial cluster on the overtopped side branch, No. 40-163, ×1.
Fig. 2. Several fertile axes. Lectotype, No. 40-92, ×1.
Fig. 3. Terminal cluster with two bisporangiate synangia, enlarged from fig. 2, ×8.
Fig. 4. Terminal cluster with poorly preserved sporangia, enlarged from fig. 2, ×8.
Fig. 5. Cluster with synangia on each of the secondary lobes, ×8.
Figs. 6, 7. Spores protruding from sporangial wall, SEM, ×200 and 350.

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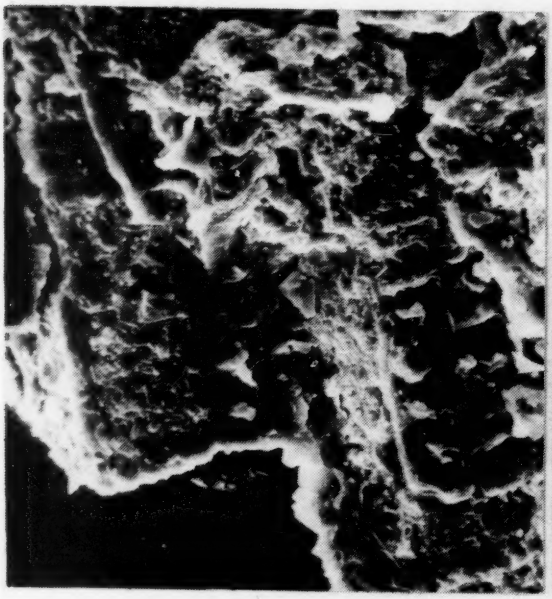

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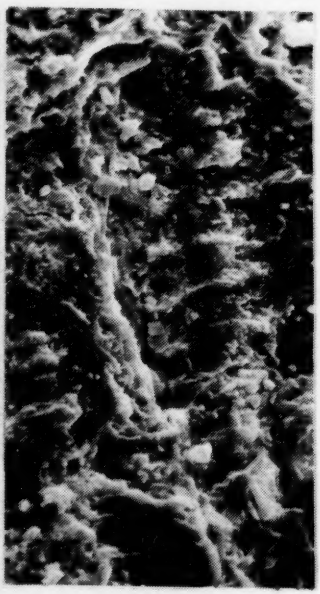

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PLATE II

omously branched axes about 1 mm thick. Branching appears as unequal dichotomy. One of the longest axes shown in Pl. I, fig. 5 is 1.1 mm wide at the proximal end, expanding slightly toward the point of dichotomy. One arm extends fairly straight for 65 mm, but shows a bulge which suggests branching at an angle to the bedding plane.

Some of the axes show a central strand of vascular tissue about 0.5 mm thick. Several fragments have been peeled along the strand and mounted for SEM. They show tracheids with spiral and annular thickenings (Pl. II, figs. 1-4).

Similar axes in Pl. I, figs. 1, 2 bear cupule-like clusters resulting from four to five rapid dichotomies. In a single specimen the cupule cluster is borne on a short side branch overtopped by a much longer axis more that 40 mm long (Pl. I, fig. 1). More typically the cupule clusters occur on unequal arms of the terminal dichotomies forming dichasial "inflorescences." The clusters have a sympodial structure resulting from successive overtopping of acroscopic appendages. Each or only the inner appendages bear sporangia (Pl. I, figs. 3-5). The appendages are striated like the main axis with conspicuous dots of hair bases.

The sporangia are about 3 mm long, 1.2 mm wide, terminal, erect, born in pairs, fused except at acute apices in bisporangiate synangia. In SEM the sporangia show spores protruding from their partly decayed walls. Spores are globose, smooth, proximally convex, with triradiate scar.

Remarks. Russian investigators have unanimously placed this material in *Moresnetia*, but differed in the species assignments. While Ananiev [1, 2] has considered his specimens from Lennyj Log conspecific with the Belgium fossils, Radczenko [5, 7] has left in *M. zalesskyi* a few rather featureless specimens from Ananiev's collection while transferring all the cupuliferous shoots to his new species *M. kryshtofovichii*. At the same time Petrosyan [7] has erected the third species *M. sibirica* for terete dichotomous axes. If nonconspecific with *M. zalesskyi*, the Siberian shoots have to be placed in *M. kryshtofovichii* as a valid binominal.

Scheckler [3], after examining a few specimens from Ananiev's collection deposited in the British Museum of Natural History, has concluded that they, though similar to *Moresnetia*, should be kept separate from this genus because other Devonian genera also differ from it in not very conspicuous details.

In *Moresnetia* asymmetric cupules are borne on unequally forked terminal branches. They contain up to four ovules which are attached in oblique vertical series. Typically the ovules are borne on the inner lobe of the third tangential division while the outer lobe divides once more, producing acute or notched tips (fig. 2). The ovules are much shorter than sterile lobes. *Lenlogia* is similar to *Moresnetia* in unequal division of fertile clusters resulting in sympodial structures

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KEY TO PLATE II

Fig. 1. Vascular tissue from the protosele of the axis, N40-94, SEM, ×400.
Figs. 2-4. Vascular elements with spiral and annular thickenings, SEM, ×1000.

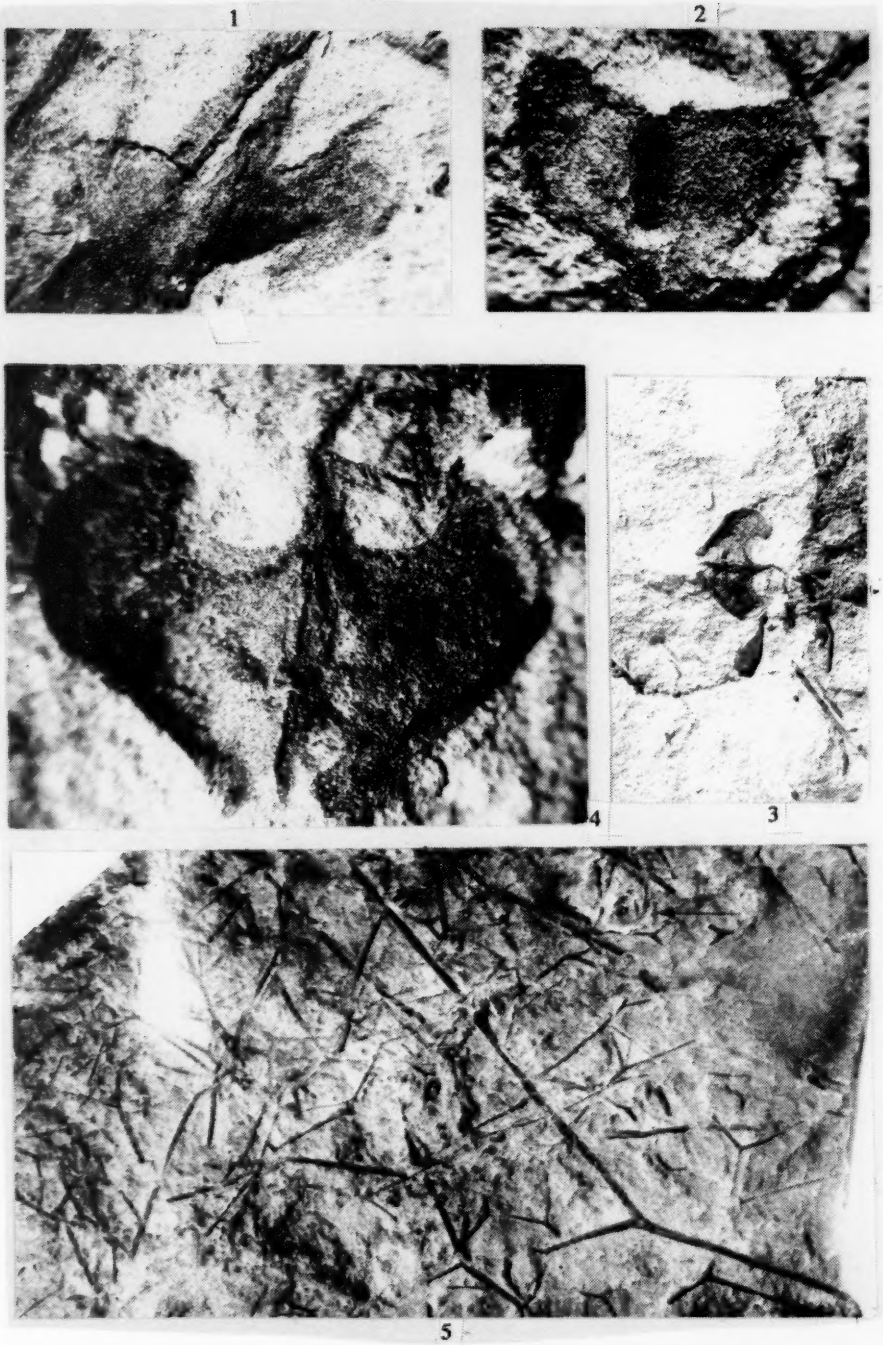

PLATE III

different from the more radially symmetrical arrangement in other Devonian seed plants, *Archaeosperma*, *Hydrosperma* and *Xenotheca*. However, in *Lenlogia* the cluster appendages bear bisporangiate sporangia comparable to those of extant *Tmesipteris*. Among the Devonian pteridophytic plants, *Protopteridophyton* is similar in having terminal clusters of paired sporangia, which are not fused, however.

RENIFORM BODIES

Ananiev found a reniform body in association with *Moresnetia*-like shoots from the Lennyj Log locality. He described it as the first Devonian seed [2]. This finding was not mentioned, however, in either of the subsequent records of Devonian seeds.

Petrosyan [5] has assigned similar reniform bodies to *Condursia* which she interpreted as a spore-bearing structure. Actually Stockmans introduced *Condursia* together with *Moresnetia* but without any implications of affinity.

Ananiev's specimen No. 40-201 (Pl. III, figs. 3, 4) occurs on a slab covered with *Lenlogia* shoots. It is 4 mm long, 8 mm wide, flat, with a thick median ridge flanked by two symmetrical lobes. On the concave side of the body the median ridge forms a collar-like protrusion with a thin flexible axis issuing from it. On the opposite end a slightly thicker axis extends from the incised base of the body. The lobes are recurved, distally pointed, thickened along the margin showing distinct arcuate lines along the concave margin.

Another similar but crumpled body was noticed among the crowded shoots on the same slab (Pl. III, fig. 3). A short axis arises from the middle of its concave side.

A smaller reniform body of the same type occurs on slab No. 40-94, also in close association with *Lenlogia* shoots. It is only 4 mm wide, less cordate, nearly triangular, with finely pitted surface (Pl. III, fig. 2). The median ridge is like in the previous specimens, 0.8 mm wide, but even more prominent, consisting of shiny coal. On the concave side there is a collar-like depression but without any issuing organ, while on the opposite end the medial ridge gives off a short tapering axis extending slightly beyond the wing.

Their interpretation as seeds still has to be confirmed. At the same time they resemble

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KEY TO PLATE III

Lenlogia kryshtofovichii and associated reniform bodies:

Figs. 1, 2. Reniform bodies preserved among the *Lenlogia* axes on specimens No. 40-94 and 40-21, ×10.

Figs. 3, 4. Reniform body showing well-developed lobes, median ridge with a collar-like protrusion and the issuing axis (Ananiev's "seed"), No. 40-201, ×2 and 10.

Fig. 5. Dichotomous axes and a reniform body (arrow), ×1.

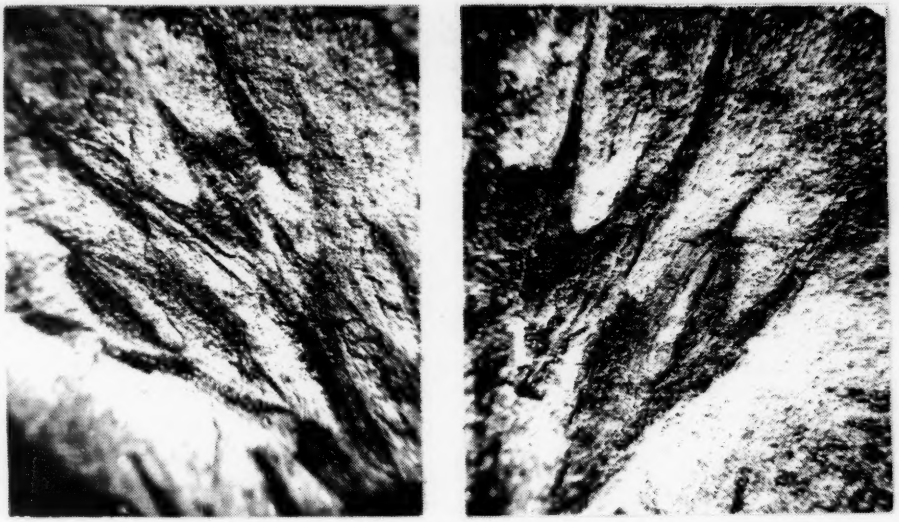

Fig. 1. *Moresnetia zalesskyi* Stockmans, Belgian specimen No. 50-3, cupules, the left one showing an ovule, ×10.

fern prothallia, which are typically reniform or cordate, flat, membranous, with an apical group of meristematic cells forming a crescent-shaped "notched" meristem which is fairly distinct from the rest of the prothallial tissue. In fossil state the notched region of densely protoplasmic cells might appear as the above-mentioned crescent-shaped areas of the reniform objects. A medial body of the latter is then positioned near the apex as archegonia in many pteridophytic plants the sporelings of which emerge through the expanded archegonium center. The primary root might grow through the prothallial tissue as in extant horsetails.

CONCLUSIONS

We conclude that Siberian species previously referred to *Moresnetia* produced sporangial clusters strikingly similar to the cupular structures of primordial ovules [4, 8].

Some interesting possibilities arise from this comparison. First, the primeval seed plants or some of them could originate from herbaceous pteridophytic progenitors remotely if at all related to progymnosperms. Further, if precursory to ovules, the *Lenlogia*-type dwarf shoots might form seed coats from the peripheral and a nucellus from the fused median sporangia. A derivation from a pair of fused sporangia—rather than a single sporangium—seems consistent with the massiveness and elaborate apical structures of the early nucelli.

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NEW SPECIES OF *Ptychocarpus* WEISS FROM THE LOWER PERMIAN OF THE MIDDLE CISURALS WITH REMARKS ON SYSTEMATICS AND MORPHOLOGY OF SOME ASSOCIATED FEATURES

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Abstract: The history of the study of Lower Permian (Artinskian and Kungurian) ferns from the Middle Cisurals, with evidence of the age and geographical position of their main localities, is presented. The sterile and fertile leaves of Artinskian and Kungurian ferns are analyzed. The sterile leaves can be divided into six morphotypes. Generative organs are distributed into four formal groups: (1) a new species of *Orthotheca* Corsin; (2) fertile leaves of ferns with poorly preserved synangia, cf. *Callymmotheca* Stur; (3) unusual fertile pinnae of Mesozoic habit, which have many characters in common with the Middle-Upper Triassic species "*Pecopteris*" *filatovae* Sixtel; and (4) ferns of Euramerican habit that have been assigned to *Ptychocarpus* Weiss. The composition and nomenclature of the *Ptychocarpus* genus are discussed. *P. distichus* Naugolnykh, sp. nov., is defined by both macromorphological and epidermal-cuticular characters.

В статье излагается история узичения некоторых раннепермских (артинских и кунгурских) папоротников Зауралья. Приведены сведения об основных местонахождениях и их возрасте. Анализируются типы стерильных и фертильных листьев из этого региона. Стерильные листья подразделены на шесть морфотипов, фертильные листья отнесены к четырем формальным группам: 1) новые виды *Orthotheca* Corsin, 2) листья с синангиями, сходные с *Callymmotheca* Stur, 3) перья мезозойского облика, сопоставимые с триасовыми *Pecopterix filatovae* Sixtel и 4) папоротники еврамерийского облика, отнесенные к *Ptychocarpus*. Новый вид *P. districhue* выделен по морфологическим и кутикулярным признакам.

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First evidence of ferns from the Lower Permian of the Middle Cisurals was published by M. D. Zalesskiy [22-25]. All of the ferns initially figured and briefly characterized (in the plate captions) by Zalesskiy [22] are from two localities: (1) the Zyurza River, Golubsovskaya Mill (actually Zalesskiy may have indicated the quarry cutting into the Krylovskaya Formation on the left bank of Zyurza River near a ruined mill in the vicinity of Aleksandrovskoe village, Kras-

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Table 1

Distribution of Artinskian and Kungurian Ferns from the Middle Cisurals

	Lower Permian											
	Artinskian Stage					Kungurian Stage						
	Upper Artinskian					Lower Kungurian			Upper Kungurian			
	1	2	3	4	5	6	7	8	9	10	11	
Fructifications												
Ptychocarpus sp.					+			+				[19]
Pytchocarpus distichus Naug., sp. nov										+		
Ptychocarpus(?) sp. 1										+		
Ptychocarpus(?) sp. 2									+			
Orthotheca sp. (sp. nov.?)										+		
Discopteris sp.							+		+?			[19]
Callymmotheca(?) sp.										+		
Asterotheca sp.										+		[9]
Sterile leaves												
Pecopteris uralica Zal.	+					+	+	+	+	+	+	
P. helenaeana Zal.									+			
P. suksunensis Zal.									cf.			
P. tchekardensis Vlad.							+		+?	+		[19, 20]
P. anthriscifolia Goepp.						+	+	+	+	+	+?	
P. kischertensis Zal.							+		+?	+?		[19, 20]
P. sp. 5 (cf. *P.* sp. AVG-1)									+			
Sphenopteris sp. 1						+	+	+	+	+	+	
Ovopteris sp.									+	+		
"*Spiropteris*" sp.										+		
Pecopteris synica Zal.										+		
P. leptophylla Bunb.		+	+									[18-20]
P. crenulata Brongn.		+		+								[18-20]
P. kruglovii Vlad.	+		+	+								[18-20]

1 - "Shaidury"; 2 - "Duvan"; 3 - "Kamenovka"; 4 - "Chernaya Gora"; 5 - "Kriulino"; 6 - "Matveyevo"; 7 - "Krasnaya Glinka"; 8 - "Krutaya Katushka"; 9 - "Chekarda-1", layer 7; 10 - "Chekarda-1," layer 10; 11 - "Chekarda-2."

Krasnoufimsk, Sverdlovsk region), and (2) Duvan village, Sylva River, Sverdlovsk region, Urminskaya Formation.

The age of the first locality was assigned by Zalesskiy to the Kungurian. The second locality is assigned to the Urminskaya Formation, which belongs to the Sargian and/or Saraninian Regional Stage of the Upper Artinskian substage [1]; its age is proven by ammonoid fauna (*Neopronorites permicus* (Tschern.) and *Uraloceras involutum* (Voin.) [1]), which are well known

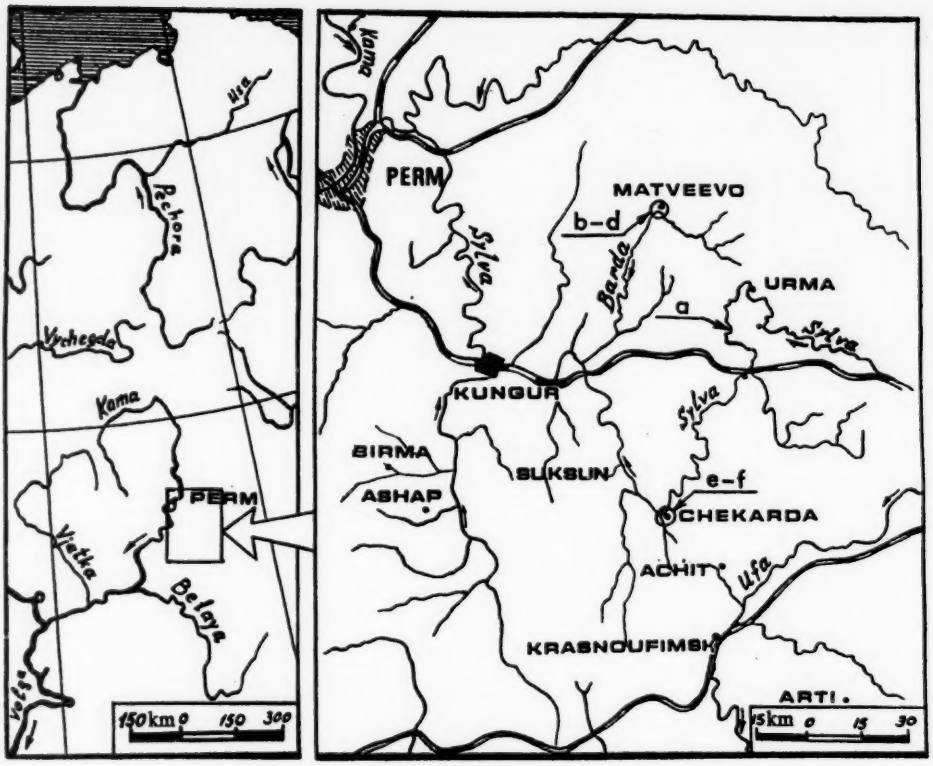


Fig. 1. Map of the Middle Cisurals indicating the studied localities. Artinskian: a - "Shaidury"; Lower Kungurian: b - "Krasnaya Glinka," c - "Matveyevo," d - "Krutaya Katushka"; Upper Kungurian: e - "Cherkarda-1," f - "Cherkarda-2."

from the Artinskian near Urma village (= Roscha village) further downstream. The latter locality also belongs to Urminskaya Formation.

A single fragment of last-order pinna from the Zyurza River locality was published by Zalesskiy and was identified as *Pecopteris* sp. [22, pl. XXXIV, fig. 6]. The pinna has small entire margined pinnules with rounded apices and a conspicuous midrib. The lateral veins are poorly preserved, but as seen on Zalesskiy's figure, most of them were simple. As a whole, this fern is quite analogous with *P. uralica* Zal., which was described from the Bardian [11] floristic complex some time later [25].

Table 2

Schematic Relationship of Main Formations of the Kungurian and Upper Artinskian (Middle Cisurals)

System	Section	Stage	Regional Stage (Horizon)	Formations		
				Barda River basin	Sylva River basin	Ufa-Aie River basin
Permian	Lower	Kungurian	Irenian	Popovskaya	Koshelevskaya	
			Filippovsky	Lek	Bardymskaya	
						Krylovskaya
		Artinskian	Saraninian	Urminskaya	Urminskaya	
			Sargian			Gabdrashitovskaya

The ferns from the Duvan locality have been assigned by Zalesskiy to *Pecopteris* and *Sphenopteris*.

Zalesskiy referred the fragment of bipinnate frond with very poorly preserved venation to *P. crenulata* Brongniart [22, XXXVI, fig. 3]. Some pinnae of this specimen are very similar to *P. uralica* Zal. Several last-order pinnae with deeply lobed pinnules and poorly preserved venation have been assigned by Zalesskiy to Euramerican species *Sphenopteris* cf. *biturica* Renault et Zeiller in open nomenclature. These specimens are very similar to another species — *Pecopteris anthriscifolia* Goeppert — which is common in the Permian of the Cisurals [2]. Another form from the Duvan is *Sphenopteris gabrielii* Zal. [22, pl. XXXVI, fig. 4]. Since the description of this species is absent from the protologus, the name of this taxon is invalid. According to its venation and general aspect of the leaf, *S. gabrielli* is not a true fern. It is quite possible that it might be a pteridosperm (callipterid?).

Later Zalesskiy described several species of sterile fern leaves from the Kungurian, which is characterized by the Bardian floristic complex containing *Pecopteris kishchertensis* Zal., *Sphenopteris pennaticisa* Zal., and other fernlike species. *P. anthriscifolia* Goepp. and *P. helenaeana* Zal., which have been described earlier, also were in the Bardian plant lists, but no detailed description or figures of these taxa were provided.

P. helenaeana was first described [23] from the Upper Permian of Bol'shaya Synya River basin. Zalesskiy supposed that this species, together with *P. anthriscifolia*, was of high

stratigraphical value, since both species are found in the same or closely contemporaneous deposits from different regions of Angaraland and the sub-Angarian ecotonal zone.

Sphenopteris pennaticisa Zal. apparently belongs to the pteridosperms, probably the peltasperms. In its general morphology it is analogous to some European species of callipterids with deeply lobed pinnules, for example, *Arnhardtia sheibei* (Gothan) Haubold et Kerp [5].

In his last big paper, which was devoted to descriptions of Bardian flora, Zalesskiy also erected two species from the sterile fern leaves, which have been considered as typical elements for this macrofloristic assemblage.

Pecopteris uralica Zal. was described from "Krutaya Katushka" locality, Lek Formation, Filippovsky Horizon, Kungurian Stage (fig. 1*d*, table 2). The holotype of this species is a fragment of a last-order pinna with 18 preserved pinnules and a complete pinna apex. The base of the pinna is destroyed. The last 2-3 pairs of the pinnules form the terminal subtriangular lobe. Every pinnule has a clear midrib and 4-5 simple or, rarely, bifurcating lateral veins. Zalesskiy pointed out that this species was similar to *P. unitus* Brongn., which is widespread in the Upper Westphalian and Stephanian of the Euramerican paleofloristic province.

Zalesskiy described *P. suksunensis* Zal., based on a fragment of bipinnate frond, from the Suksunskiy Formation, which is correlated to the Upper part of the Koshelevskaya Formation of Irenian Horizon (Upper Kungurian substage). Last-order pinnae of this species bear deeply lobed pinnules with a distinct midrib. Every lateral vein runs into a lobe and branches once near its base; the anadromic (frontal) branch of the lateral vein has its next bifurcation near the margin of the pinnule. Lateral veins of the distal part of the pinnules branch only once. This species is endemic. There are no obvious taxonomic affinities of *P. suksunensis* in other regions.

Zalesskiy did not indicate any finds of fern fructifications from the Lower Permian of the Middle Cisurals.

In his summary paper on characteristics of the Permian floras of the Cisurals and the Russian platform, S. V. Meyen [8] noticed that "ferns are very rare for Kungurian flora." Some time later Meyen published a figure of a fertile last-order pinna [9], identified as *Asterotheca* sp., from the "Chekarda-1" locality (figs. 1*e*, 2*B*; table 1), which belongs to the Koshelevskaya Formation.

In a number of papers on Lower Permian floras of the Urals and the Cisurals, V. P. Vladimirovich [18-20] identified several species of *Pecopteris*. Some, for example, *P. leptophylla* Bunb., are characteristic of both the Upper Artinskian and Lower Kungurian. *P. kischertensis* Zal., *P. crenulata* Brongn., and *P. kruglovii* Vlad. are typical for the "Saraninian-Filippovian" complex (Vladimirovich assigned the Saraninian Horizon to Lower Kungurian). *P. tchekardensis* Vlad. was described by Vladimirovich from the "Chekarda-1" locality. It has bipinnate fronds with closely spaced last-order pinnae, and its pinnule margins are slightly lobed. The venation of *P. tchekardensis* is similar to that of *P. suksunensis*. Vladimirovich compared *P. tchekardensis* with, in her opinion, closely related species *P. leptophylla*, which differs from *P. tchekardensis* in smaller pinnules and simpler venation.

A large collection of Artinskian and Kungurian ferns from several different regions of the Middle Cisurals (fig. 1) was made by this author. The Artinskian ferns are characterized by poor

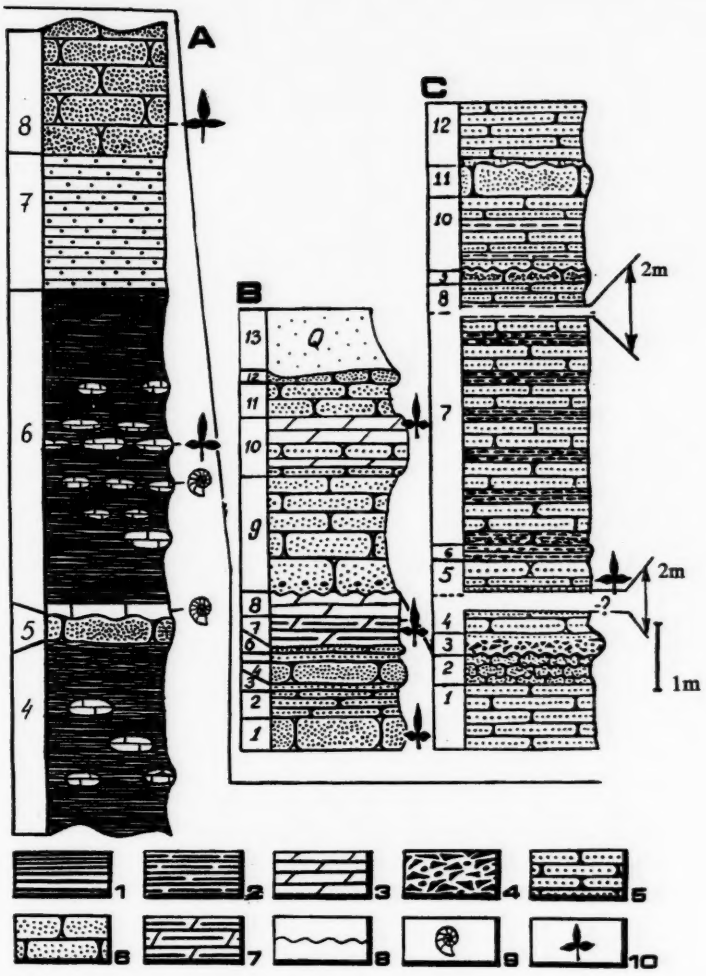
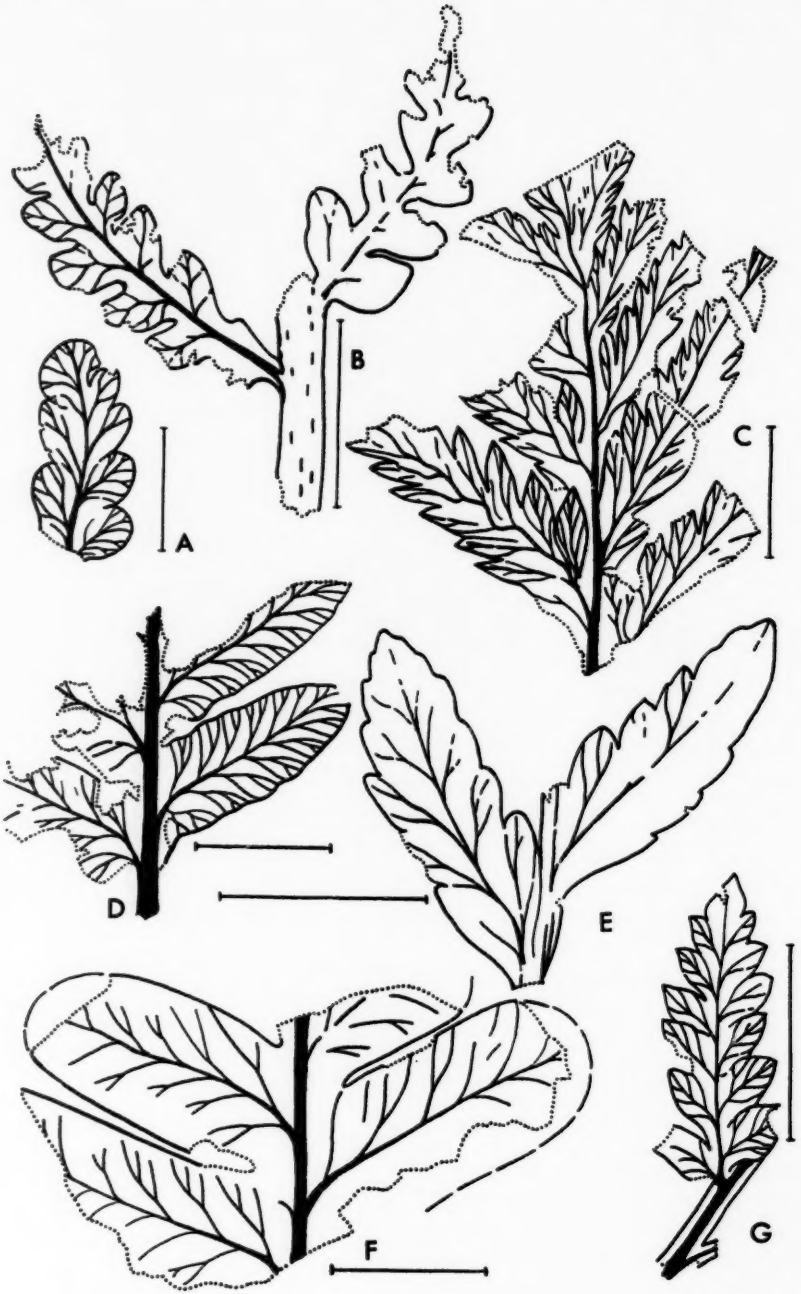


Fig. 2. Stratigraphical sequences of the most representative localities of Upper Artinskian (A) and Upper Kungurian (B, C). A - "Shaidury," B - "Chekarda-1," C - "Chekarda-2." Legend: 1 - argillite, 2 - aleuropelite s.s., 3 - marl, 4 - breccia, 5 - aleurolite, 6 - sandstone, 7 - clayey marl, 8 - surface of discontinuity, 9 - ammonoids, 10 - macrofloristic remains.

preservation in comparison with Kungurian ones. Details of venation and sometimes even contours of pinnules are poorly preserved. It can be said with some confidence that both pecopteroid and sphenopteroid forms are among these specimens, but the European species (such as *P. leptophylla* and *P. crenulata*) indicated in Vladimirovich's lists cannot be identified nor can they be assigned to the endemic Uralian taxa.


A
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E
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G

The only exception is a single fragment of last-order pinna, from the Urminskaya Formation ("Shaidury" locality, figs. 1*a*, 2*A*; table 1), which is assigned to *P. uralica*. Traditionally [19, 20, 25], this species has been regarded as typically Bardian (i.e., Kungurian); thus, its correct identification from the true Artinskian deposits, which are characterized by rich ammonoid fauna [1], is important from a stratigraphical point of view.

The best Lower Permian ferns from the Middle Cisurals are from the Kungurian of the Sylva River basin (fig. 1*b-f*). Well-preserved samples were found in "Chekarda-1" and "Chekarda-2" localities (fig. 2*B-C*). The ferns are both sterile and fertile. Sterile leaves are very heteromorphic and can be divided into several groups by macromorphological characters.

Macromorphological groups of sterile fern leaves from the Kungurian of the Middle Cisurals

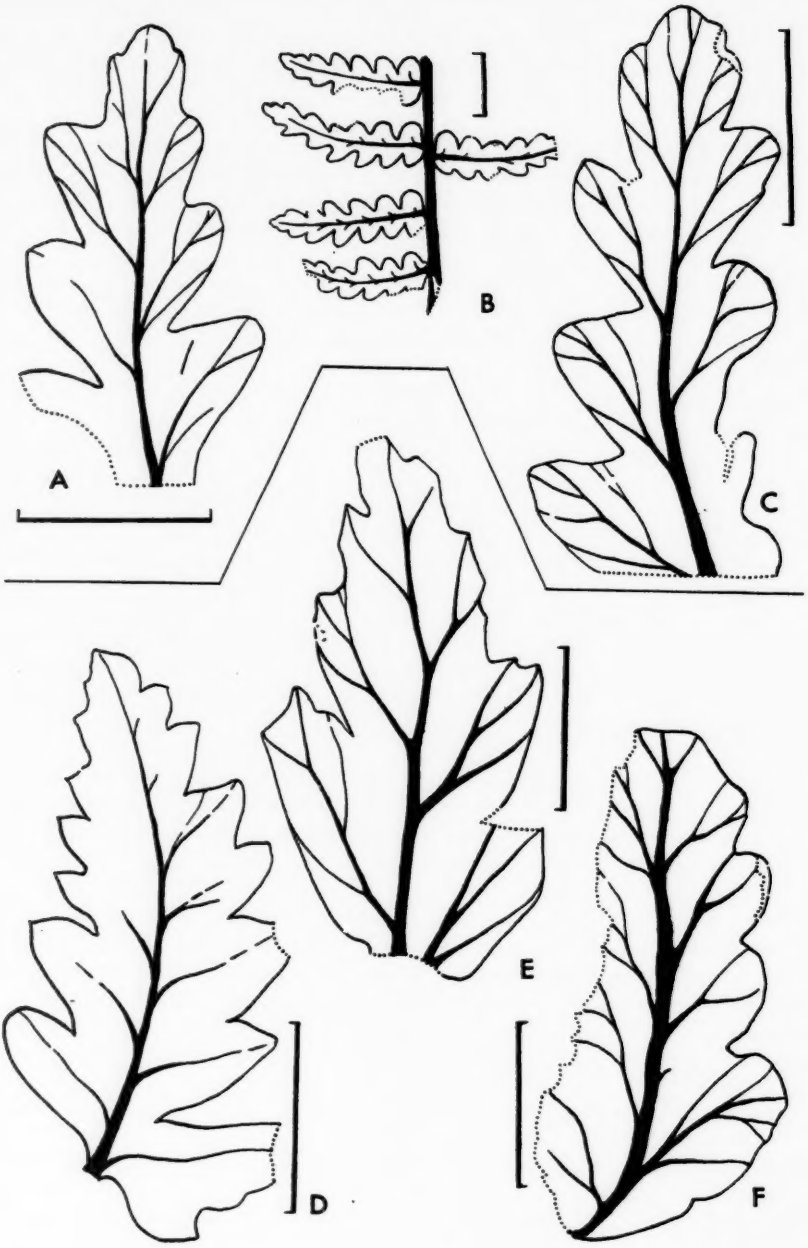
1. The first group includes fern leaves with entire margined pinnules. The pinnule apex is rounded. Wings of the pinna rachises are differently developed. *P. uralica* Zal., with simple lateral veins, and *P. helenaeana* Zal., with more complicated venation (figs. 3*D*, *F*, and 6*B*, *C*) belong here. It should be noted that typical specimens of *P. helenaeana* Zal. from B. Synya River basin [23, figs. 6-9] have simpler venation (once-branched lateral veins) than the Kungurian representatives of this species. L. A. Fefilova [2] described *P. helenaeana* from the Upper Permian of Adz'va, Perebor, Pechora, Vorkuta and B. Synya river basins (Pechora Cisurals), whose leaves combine both types of venation in one fragment of a single frond [2, fig. 18*a*].

2. The second group includes sterile leaves with pecopteroid pinnules, which have undulate or lobed margins, rounded apices, and pinnate venation of different types (commonly with once- or twice-branched lateral veins). These leaves are assigned to *P. anthriscifolia* Goepp., *P. tchekardensis* Vlad., and *P. suksunensis* Zal.

3. The third morphological group contains sphenopteroid leaves with dissected margins, acute apices of lobes, well-developed midrib of the pinnules, and lateral veins bifurcating 3-4 times. The leaves are commonly preserved as isolated pinnules (fig. 4*D-F*). I identified these pinnules as *Sphenopteris* sp. 1, due to incompleteness of the materials.

4. An unusual group of Kungurian sterile fern leaves from the Middle Cisurals consists of a number of last-order pinnae with lobed ovoid pinnules, and developed wings of the pinna rachis (fig. 6*D*). The venation of these pinnules is typical of Kungurian ferns. The same type of venation is observed in *P. tchekardensis* and *P. suksunensis*: a branched lateral vein runs into every lobe of the pinnule. The frontal (anadromic) branch of the bifurcated lateral vein branches 1-2 times again. Lobes of the pinnule are further slightly lobed. Small lobes (second-order lobes)

Fig. 3. Main morphotypes of Kungurian sterile leaves from the Middle Cisurals: A - *Pecopteris* sp. 1, spec. No. 3773(11)/250a(90); B - *Pecopteris* sp. 2, spec. No. 3773(11)/335(93); C - *Pecopteris synica* Zal., spec. No. 3773(11)/267(91); D - *Pecopteris helenaeana* Zal., spec. No. 3773(11)/270(91); E - *Pecopteris* sp. 3, spec. No. 3773(11)321(92); F - *Pecopteris helenaeana* Zal., spec. No. 3773(11)/61(89); G - *Pecopteris* sp. 4, spec. No. 3773(11)/266(91). "Chekarda-1": A-B, E - layer No. 7; C-D, F-G - layer No. 10. Scale: A-E, G - 1 cm, F - 0.5 cm.


A
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are especially developed near the apices of the normal lobes (first-order lobes). The ends of the lateral veins run into apices of the small lobes (second-order lobes). Similar leaves are known from the Carboniferous and Lower Permian of the Euramerican province and belong to *Ovopteris* Potonie. My material was tentatively identified as *Ovopteris* sp. [11, pl. II, fig. 3] in open nomenclature.

5. Isolated leaves assigned to *P. synica* Zal. form the fifth group of the sterile fern leaves. These leaves commonly are the fragments of bipinnate fronds with subtriangular pinnules. Usually, the pinnules are strongly connected by their bases. Apices of the pinnules vary from acute to slightly rounded. Venation is relatively simple: every pinnule has 1-3 pairs of opposite lateral veins arising from a well-developed midrib. The rachises of last-order pinnae are slightly undulating (fig. 3*C*). It is possible that the fragment of last-order pinna with closely similar epimorphology and venation, but different from *P. synica* in the structure of pinna rachis, belongs to the same form group. A more consolidated black axis zone and two thinner lateral zones that connected with the axis along both its sides are in these fern leaves, preliminarily determined as *Pecopteris* sp. 4 (fig. 3*G*) in open nomenclature.

6. One fern, atypical and rare for Kungurian of the Middle Cisurals, was assigned to *Pecopteris* sp. 5 (cf. *P.* sp. AVG-1 [3]). The single fragment of bipinnate frond has five last-order pinnae. The main rachis is slightly curved. The last-order pinnae are almost opposite and flexed by their apices toward the frond apex. The pinna bases extend without any recurrence. Rachises of the last-order pinnae arise from the main rachis approximately under 90°. Entire margined pinnules are almost opposite, closely spaced and fused at their bases. Basal pinnules have widely rounded apices. On more distal parts of the pinnae are pinnules with slightly acute apices. Near the apex of the last-order pinna the pinnules are fused by their margins and form the terminal pinnule with lobed margins (fig. 4*A-C*). This specimen is similar to *Pecopteris* sp. AVG-1 from the Upper Tartarian of the Russian platform [3] in general habit and construction of the frond, but my leaf has simpler venation.

In addition to the above six main morphotypes of the sterile fern leaves from Kungurian of the stratotype region, my collection has a number of small, poorly preserved fragments (for example, fig. 3*A-B, E*); these, on the one hand, do not correlate with the groups mentioned and, on the other hand, the characters by which one could form one or several other formal groups for them are not sufficient. These ferns contain different small pecopteroid pinnules, rachises with destroyed pinnules, and so on. One terminal fragment of a juvenile sterile pinna, identified as "*Spiropteris*" sp., is a last-order pinna. It has a circinate distal part and small underdeveloped pinnules on the inner side of the spiral, and bigger ones on the proximal part of the pinna.

The types of generative leaves of the Kungurian ferns have remained unknown for a long time because of their rarity. Nevertheless, my collection allows characterization of some fertile pinnae, which can be divided into four types: (1) synangia, formed by connate sporangia, disposed

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Fig. 4. Main morphotypes of Kungurian sterile fern leaves from the Middle Cisurals. A-C - *Pecopteris* sp. 5 (cf. *P.* sp. AVG-1), spec. No. 3773(11)/149(89); D-F - *Sphenopteris* sp. 1; D - spec. No. 3773(11)/258(90); E - spec. No. 3773(11)/248(90); F - spec. No. 3773(11)/247(90). "Chekarda-1": A-C - layer No. 7, D-F - layer No. 10. Scale: B - 1 cm, A, C-F - 0.5 cm.

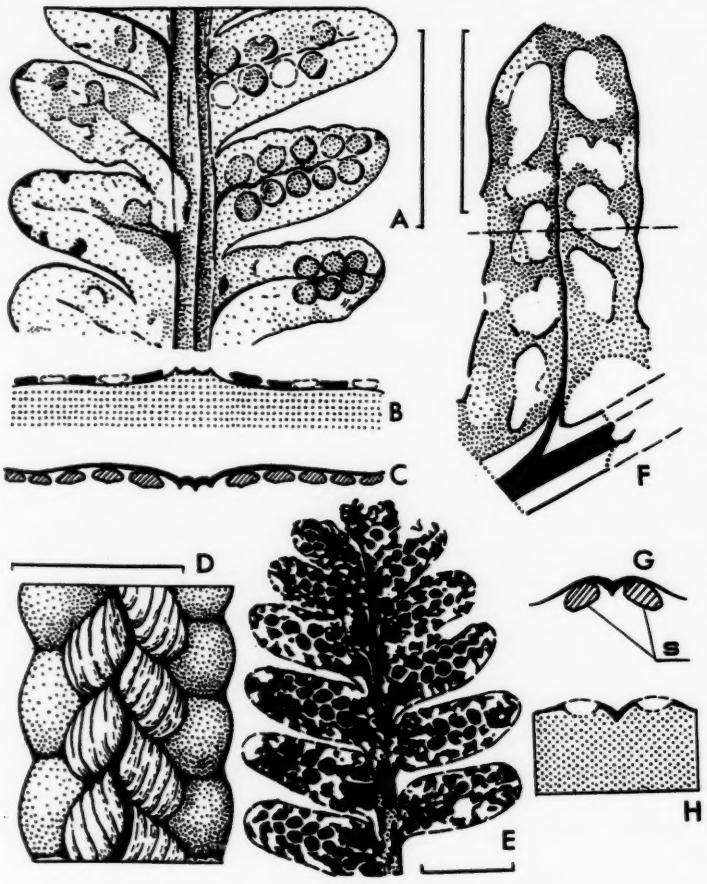

Fig. 5. Kungurian fertile fern leaves from the Middle Cisurals. A - *Ptychocarpus distichus* Naugolnykh, sp. nov. holotype No. 3773(11)/27(89); B - schematic cross section through same pinna, on matrix with abaxial surface uppermost; C - cross section of reconstructed pinna with abaxial surface downward; E - *Ptychocarpus* (?) sp. 1, scheme of abaxial surface of fertile pinnule, spec. No. 3773(11)/286(91); E - *Ptychocarpus* (?) sp. 1, general structure of terminal part of fertile last-order pinna, spec. No. 3773(11)/286(91); F - *Ptychocarpus* (?) sp. 2, fertile pinnule, spec. No. 3773(11)/255(90); G - schematic cross section through same reconstructed fertile pinnule, *s* - synangia; - cross section through fertile pinnule on matrix with abaxial surface downward and with destroyed synangia. "Chekarda-1": A-E - layer No. 10, F-H layer No. 7. Scale: A-C, F, E - 0.5 cm, D - 0.3 cm, G, H - without scale.

in the middle and distal parts of the once-branched lateral veins of the fertile pinnules; (2) synangia formed by sporangia which are joined at their bases, and disposed on lateral veins (1-2 synangia on every pinnule) irregularly; (3) fertile pinnules characterized by pinnate venation with simple lateral veins, with every lateral vein having terminal sporangium; and (4) synangia forming two regular lines along the midrib on the abaxial surface of the fertile pinnule.

The single pinna assigned to the first category was preliminarily identified by the author as *Orthotheca* sp. (sp. nov.?) [10, 11, pl. I, 4]. This specimen differs from *O. petschorica* Fefilova [2] from the Upper Permian of the Pechora Basin by the more distal dichotomy of the lateral vein forming a "stalk" with two second-order lateral veins that have two lines of elongated sporangia; also in the absence of paired disposition of pinnules and lateral veins; and in the position of the midrib being nearer to the anadromic (frontal) margin of the fertile pinnule (fig. 6*E*). Our specimen differs from the type species *O. saraepontana* Corsin in having fewer lateral veins.

The second type of fertile leaves is related to the Lower Carboniferous (!) Euramerican genus *Callymmotheca* Stur, but this relationship may be only superficial (fig. 6*G*).

The third type of fern fructifications is a single specimen of a fertile last-order pinna with very small (possibly underdeveloped) sporangia (fig. 6*F*) on the ends of the simple lateral veins. My specimen is similar to the pinna described by T. A. Sixtel [16] as *Pecopteris filatovae* Sixt. from Madygenskaya Formation (Middle Upper Triassic) of Uzbekistan.

The fourth type of fertile ferns is similar to *Ptychocarpus* Weiss (figs. 5, 6*A*, pl. II). These generative leaves are remarkably similar to the Upper Carboniferous Euramerican species *Pecopteris unitus* (Brongn.) Zeiller. These Kungurian forms are described below as *Ptychocarpus distichus* Naugolnykh, sp. nov., *P.* (?) sp. 1, and *P.* (?) sp. 2.

The composition and nomenclature of *Ptychocarpus* Weiss

The history of the nomenclature and the composition of *Ptychocarpus* are rather intricate. *Pytchocarpus* was erected in 1869 by C. E. Weiss [21]. The type species, *P. hexastichus*, is from the Upper Carboniferous (Stephanian?) of West Prussia, and the holotype is a fertile bipinnate frond. Every pinnule is 3.5 cm long and 0.8 cm wide, and has six lines of ovoid synangia (?), which are transverse to the midrib of the fertile pinnule. Thus, every pinnule produces three lines of synangia from each side on the fertile pinnule, on its abaxial surface, and along the midrib. Some synangia, in the specimen figured by Weiss [21, pl. XI] show extended furrows. *P. hexastichus* is similar to sporophore of "*Pecopteris-Marathiotheca*" Grand'Eury [4, pl. VII, fig. 5*b*, *c*]. If such correlation is correct, the synangia of *Ptychocarpus hexastichus* were dissected by furrows into two parts. *Marathiotheca* has eight sporangia (every segment of synangia contains four sporangia). It is possible that the synangia of *P. hexastichus* have the same number of sporangia.

B. Renault and R. Zeiller in 1988 [14] assigned the fructifications associated with the sterile fronds of *Pecopteris unitus* Brongn. to *Ptychocarpus*. Fertile pinnules of *Pecopteris unitus* have two lines of synangia which are disposed along the midrib on the abaxial surface of the pinnule. Every synangium has a depression in its center and is traversed by small radial furrows and ribs. The only important similarity between *Ptychocarpus hexastichus* and *Pecopteris unitus* is the regular arrangement of synangia in lines along the midrib of fertile pinnules. A few years later Renault

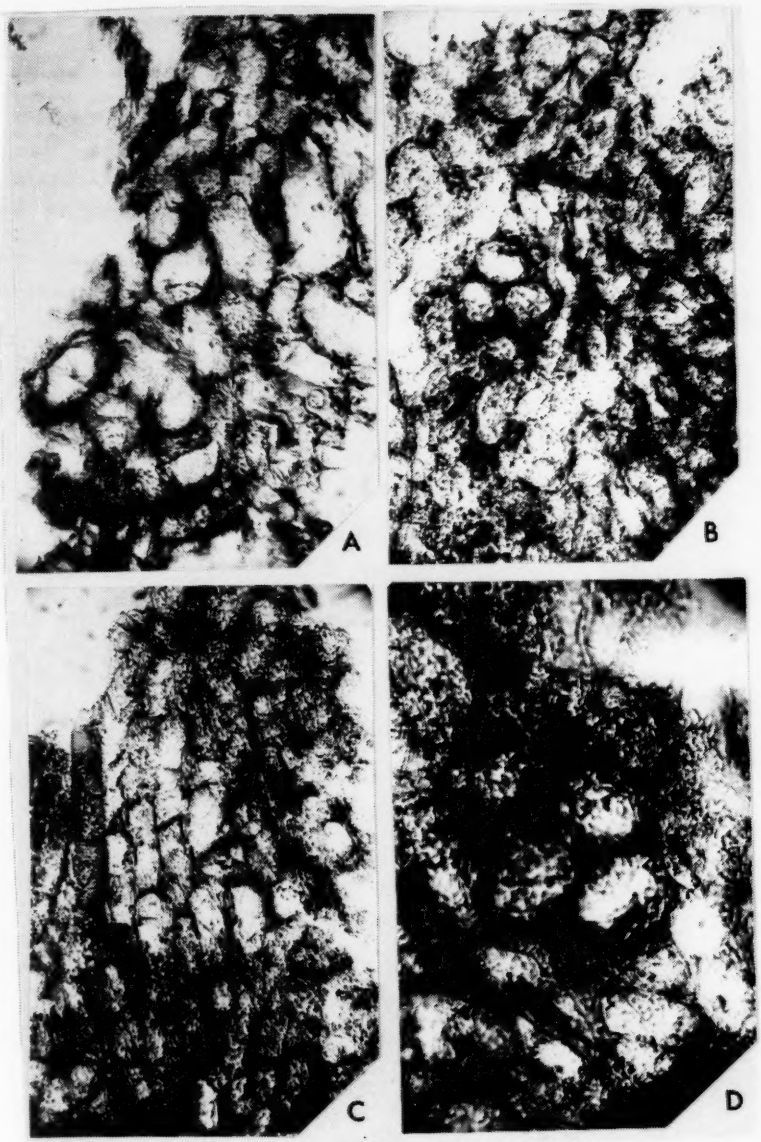

PLATE I

KEY TO PLATE I

Ptychocarpus distichus Naugolnykh, sp. nov. Cuticular structure. A-C, ×200, D, ×500. A - slide No. 3773(11)/27(90)B; B-D - slide No. 3773(11)/27(90)A. "Chekarda-1," layer No. 10. Explanation in text.

[12-13] described petrified fronds of *P. unitus* and gave a more detailed description of this taxon. He proposed *P. unitus* as the type species of *Ptychocarpus* Weiss, but this suggestion contradicts the priority rule of ICBN.

Evidently, the difference between *Ptychocarpus hexastichus* and *Pecopteris unitus* is remarkable. Nevertheless, A. C. Seward [15] remarked that these species are closely related.

The situation became even more difficult after the description of *P. oblongus* Kidst. from the Upper Carboniferous of Camerton (England) by R. Kidston [6]. This species was established on two bipinnate fertile fronds without limbs. Every pinnule bears 3-4 pairs of pinnules, which have several synangia arranged in two lines along the pinnule midrib. Every synangium may have consisted of two sporangia, but it is next to impossible to give detailed characteristics of the synangial structure because the material is poorly preserved. When describing *P. oblongus*, R. Kidston noted its formal reference to *Ptychocarpus*.

Some time later other species were assigned to *Ptychocarpus* (see, e.g., [7], etc.). The main characters that combined these fructifications into a single genus are the following: (1) disposition of synangia in 1-3 lines along the midrib on both sides of abaxial surface of fertile pinnule; (2) compound, commonly bipinnate frond; and (3) relatively simple venation of sterile leaves.

Obviously, the genus *Ptychocarpus* is a formal heterogeneous taxon, and in need of revision. Nevertheless, the author considers it expedient to use this genus for some Paleozoic ferns that are similar to *Ptychocarpus hexastichus* or *Pecopteris unitus* but their poor preservation does not allow a detailed study of the microstructure and anatomy of reproductive organs.

Ptychocarpus Weiss, 1869

Ptychocarpus distichus Naugolnykh, sp. nov.

Pl. I, A-D, Pl. II, A-C

Derivation of name. *distichus* (Greek) - two lines (referring to two lines of synangia on abaxial surface of fertile pinnule).

Holotype. No. 3773(11)/27(89) - Geological Institute, Russian Academy of Sciences; Middle Cisurals, Perm region, left bank of Sylva River, downstream of Chekarda River mouth, "Chekarda-1" locality, layer 10; Lower Permian, Kungurian Stage, Irenian Horizon, Koshelevskaya Formation.

Description (fig. 5*A*, *C*). The better preserved specimen, selected as holotype, is large fragment of fertile bipinnate frond, 68 mm long, and more than 70 mm wide. Entire width is unknown, for distal parts of last-order pinnae are absent on one side of frond. Lower surface of frond faces observer. On some parts are compression fragments. Other parts of holotype are impressions of upper (adaxial) surface of frond.

Frond rachis is about 2.5 mm thick, with fine transverse ribs and furrows. In middle of rachis is longitudinal furrow, which is subtriangular in cross section (fig. 5*B-C*). On lower

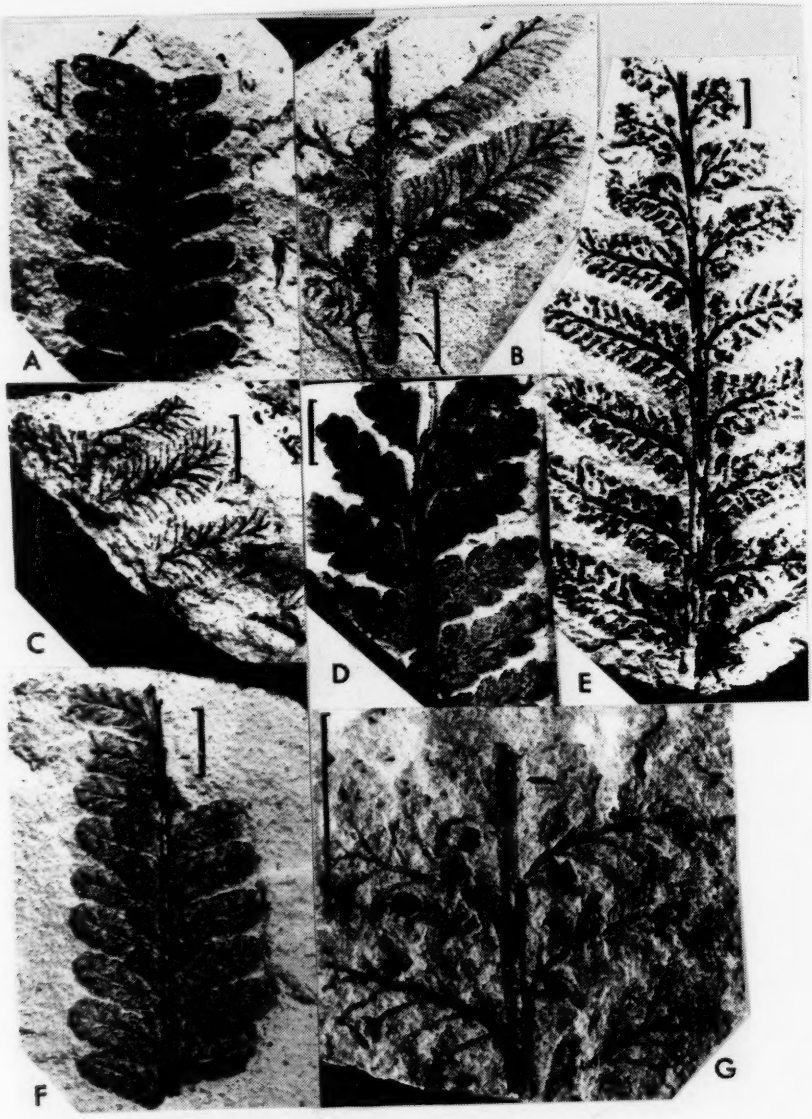

Fig. 6. Kungurian ferns from the Middle Cisurals. A - *Ptychocarpus* (?) sp. 2, spec. No. 3773(11)/255(90); pinnule pointed out by arrow shown in Fig. 5F; B-C - *Pecopteris helenaeana* Zal., B - spec. No. 3773(11)/270a(91), C - spec. No. 3773(11)/15(89); D - *Ovopteris* sp., spec. No. 3773(11)/288(91); E - *Orthotheca* sp. (sp. nov.), Spec. No. 3773(11)/291(91); F - fertile pinna similar to *Pecopteris filatovae* Sixt., spec. No. 3773(11)/293(91); G - fragment of fertile pinna of *Callymmotheca* (?) sp., spec. No. 3773(11)/318(92). A - "Chekarda-1," layer 7; B-G - "Chekarda-1," layer 10. Scale: 0.5 cm.

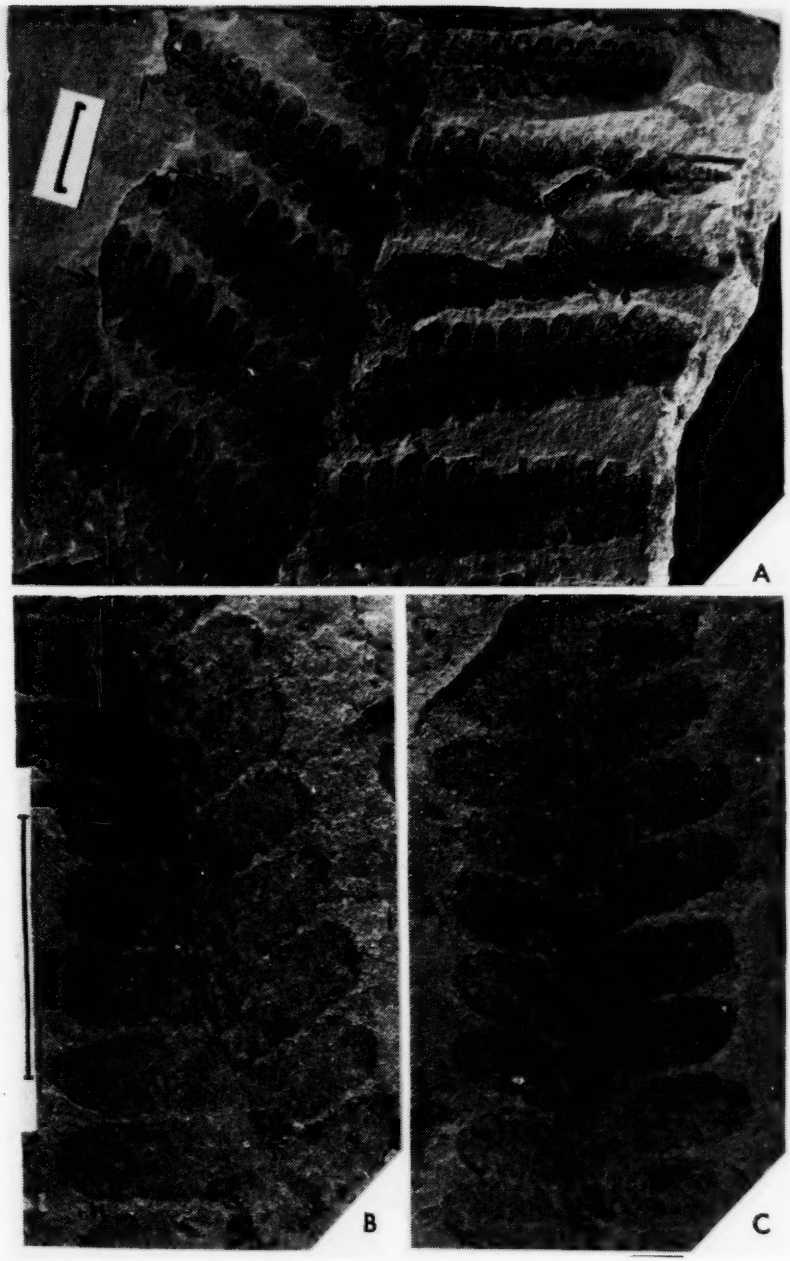

PLATE II

KEY TO PLATE II

Ptychocarpus distichus Naugolnykh, sp. nov. Holotype, No. 3773(11)/27(89). A - general view, B-C - detail of last-order pinnae. "Chekarda-1," layer 10. Scale = 1 cm.

(abaxial) surface of rachis, this furrow corresponds to longitudinal rib which is prominent on holotype (fig. 5*A*).

Last-order pinnae arise from frond rachis at angle of 60-70°. Length of each pinna is about 40 mm; maximal width of basal part of pinna is 10 mm. Rachises of last-order pinnae show rib on their adaxial surfaces, like frond rachis.

Synangia are rounded, approximately 1 mm in diameter. There are up to 10 synangia per pinnule. On each side of midrib are 5 abaxial synangia.

Several cuticular fragments with preserved sporangia have been macerated from holotype.

The first cuticular type is characterized by epidermal cells with ovate outlines. Cell walls are slightly flexed toward outer sides or undulated. Length of cells is 40-70 μm, width is 30-40 μm. Cells are slightly oriented in one direction by their long axes (pl. I, A).

The second cuticular type is characterized by smaller epidermal cells than those of first cuticular type. Cells have rectangular contours, 40-50 μm long, 20-25 μm broad. Cells extend in one direction. Transverse walls are oblique to long walls, forming "brick work" (pl. I, C).

Evidently, these two cuticular types characterize both leaf sides of fertile pinnule. It is possible that one cuticular fragment belongs to the upper surface of the leaf, and the other to the lower surface. However, I cannot rule out another possibility: the first cuticular type might represent intercostal areas of the leaf, and the second might belong to costal areas. Unfortunately, existing materials cannot provide an unequivocal answer to this question.

Cuticles of the third type, from the same specimen, obviously belong to sporangium walls. In one slide (pl. I, B, D) scar of tetrad spora was found.

Plate I, B shows radially arranged rounded or slightly elongated cells supposedly corresponding to placental area of a synangium.

Comparison and Remarks. Other *Ptychocarpus*-like forms are known from the "Chekarda-1" locality. They are listed here as *Ptychocarpus*(?) sp. 1 (fig. 5*D*, *E*) and *P.*(?) sp. 2 (figs. 5*F-H*, 6*A*). *P.*(?) sp. 1 differs from *P. distichus* in its ovoid form of the synangia, undulated midrib of pinnules, and in presence of fine ribs on synangium abaxial surface. *P.*(?) sp. 2 obviously is related to *P.*(?) 1, but differs from the latter specimen by less lobed pinnule margins and by apparently more elongated synangia.

New species differ from closely related *Pecopteris unitus* (Brongn.) Zeiller in number of synangia on each fertile pinnule. Commonly, three synangia are in one line on *P. unitus* and on *Ptychocarpus distichus*, five synangia.

Material. Holotype and two topotypes.

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Scytophyllum AND THE ORIGIN OF ANGIOSPERM LEAF CHARACTERS

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Abstract. Peltasperm leaves from the uppermost Triassic of the Eastern Ural Ranges are assigned to *Scytophyllum vulgare* (Prynada) Dobruskina. Detailed study of venation in cleared compressions has revealed vascular conservatism as well as restructuring of original venation in the marginally fused (coherent) leaf segments. Restructuring in the direction of original cladophleboid venation is described as retroconvergence. Incipient areolate venation appears in the bicoherent portion of the leaf blade. It is hypothesized that both plate meristem and reticulate venation have resulted from modified activity of the fusion meristem.

Листья папоротников из верхнего триаса Восточного Урала отнесены к *Scytophyllum vulgare* (Prynada) Dobruskina. Детальное изучение жилкования на просветленных фитолеймах позволило установить консерватизм жилкования и проследить его перестройку в когерентных листьях. Перестройка в направлении исходного кладофлебоидного жилкования описана как ретроконвергенция. В бикогерентной части листа намечается образование сетчатого жилкования. Предполагается, что пластинчатая меристема и сетчатое жилкование возникли на основе меристемы слияния в когерентных листьях.

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Introduction

Since Goethe, the leaf has been considered a basic unit of plant morphology; however, the leaf itself is enigmatic, and its origin remains obscure. Among extant plants, angiosperms are unique in the developmental complexity of their leaves. Initially they develop similarly to the fern leaves, but then grow by cooperation of different meristems, suggesting a compound organ.

Several groups of lower seed plants have fernlike foliage. Some of them, though remotely related to angiosperms, have acquired angiosperm-like features by parallel evolution [1]. Among them, the extinct late Paleozoic-Early Mesozoic gigantopterids and peltasperms are characterized by the "coherence" of their leaf segments which are marginally fused but maintain their original pattern of venation. Leaf coherence was first described by Asama [3] in *Gigantopteris* and its allies as a special case of phylogenetic fusion, and later was studied by Dobruskina (1969) in *Scytophyllum*, a peltasperm leaf-genus. Gigantopterids and peltasperms can be seen as sister

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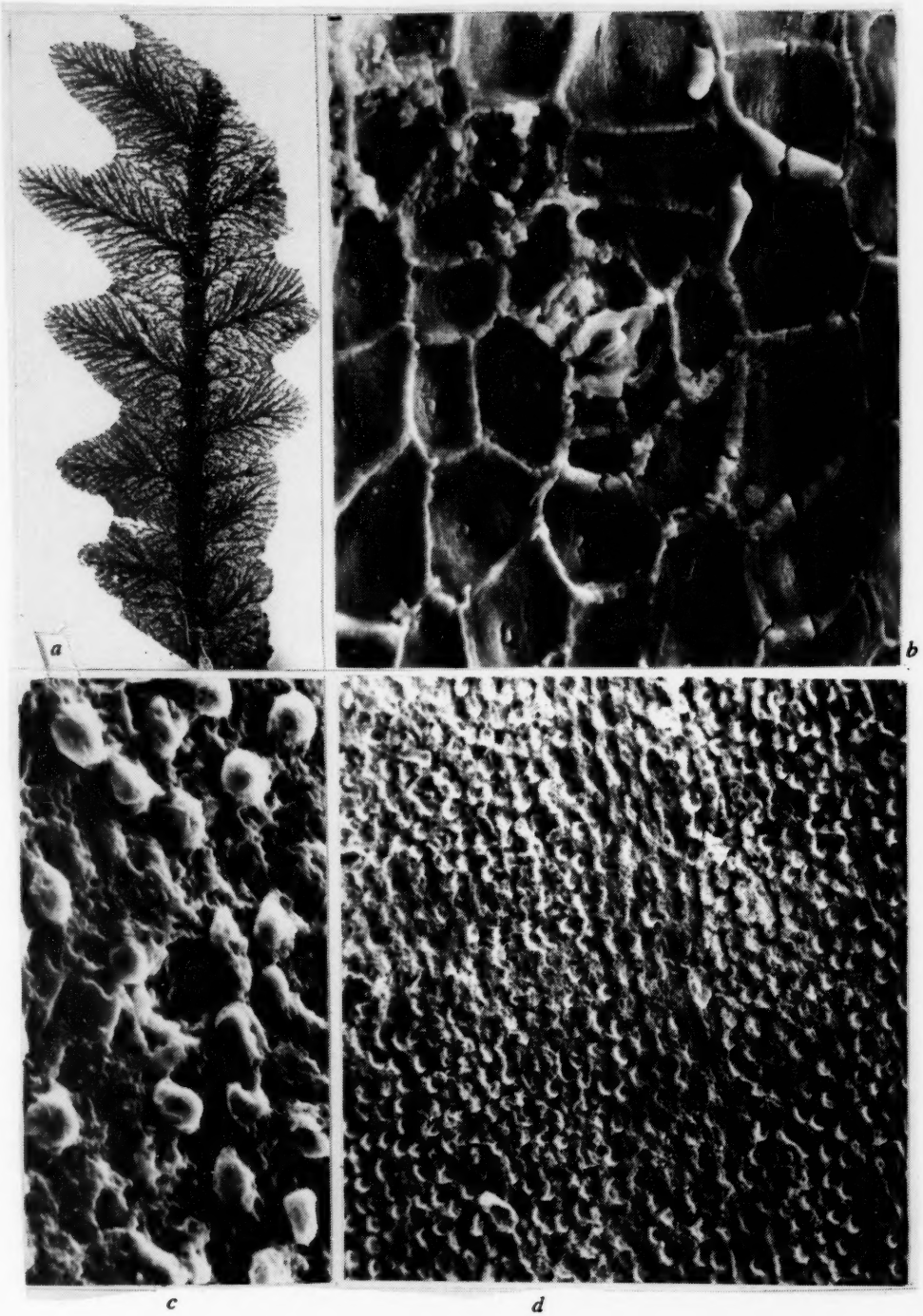
a
b
c
d

groups (Krassilov, 1989) in which leaf coherence evolved independently in the course of parallel evolution. Moreover, both the gigantopterid and peltasperm lines tend towards reticulate venation typical of angiosperms.

Studies of fossil leaf morphology thus seem pertinent to the fundamental problems of plant evolution, such as the appearance of new leaf types, new meristems, closed venation as well as parallel evolution, and differential rates of evolutionary change in leaf characters. These problems are discussed below in relation to *Scytophyllum vulgare*, a peltasperm showing incipient areolate venation.

Scytophyllum vulgare (Prynada) Dobruskina

Thinnfeldia vulgaris: Prynada, 1940, [11] p. 24, figs. 1, 3; Vladimirovich, 1965, [15] p. 241, pl. 2, figs. 1-8; pl. 3, figs. 1-2.

Locality. In 1939 V. D. Prynada found above the coal bed at Bogoslovsk coal mine in the eastern Ural Ranges a lens of marly clays containing abundant leaf compressions, mostly fernlike pinnate leaves of "*Thinnfeldia*" *vulgaris* associated with *Furcula, Czekanowskia, Phoenicopsis, Podozamites,* and *Cycadocarpidium*. The age of the plant bed was given as latest Triassic (Rhaetian). Compressions were cleared by immersion for an hour in HCl or HNO_3.

Taxonomy. Prynada [11] figured two specimens under the name *Thinnfeldia vulgaris*, which was accepted also by Vladimirovich [15] in her fuller description of the species. However, *Thinnfeldia* is a leaf-genus for noncoherent leaves. It is similar if not synonymous to *Pachypteris*, another noncoherent leaf morphotype.

Dobruskina [4] mentioned (p. 42) "*Thinnfeldia*" *vulgaris* as a possible representative of *Scytophyllum*, a peltasperm genus with coherent leaves. "*T. vulgaris*" is obviously similar to a number of leaf morphotypes described as *Scytophyllum* by Linnel [10], Dobruskina [4, 5] and Khramova [8], and also as *Lepidopteris stormbergensis* Townrow and *L. africana* (Du Toit) Holmes [2]. Zamuner and Artabe [16] have suggested a derivation of *Scytophyllum* from *Lepidopteris* with *L. madagascariensis* and *L. stormbergensis* as transitional forms. In both *Scytophyllum* and *Lepidopteris*, which are obviously overlapping genera, venation is described as open, while in "*T.*" *vulgaris* anastomosing and looping of the veins seem more than occasional. This distinction is hardly enough, however, for separation on the generic level.

Fig. 1. *Scytophyllum vulgare*, leaf morphology and epidermal structure: *a* - pinna with interstitial pinnules incorporated in coherent proximal part of lamina, ×2; *b* - stoma, internal view, SEM, ×400; *c* - stoma, external view, SEM, ×400; *d* - upper cuticle with costal zone of filed cells and intercostal zones of papillate cells and stomata, SEM, ×200.

Fig. 2. *Scytophyllum vulgare*, venation of coherent pinnules: *a* - pinnule with fasciculate proximal veins and dichotomous distal veins, ×3; *b, c* - parts of (*a*) enlarged to show short branches of fasciculate veins approaching each other. Note an interstitial vein and an occasional loop in (*b*), ×7; *d* - pinna with well-defined interstitial pinnule, ×2.

Leaf Morphology

Leaves supposedly bipinnate, pinnae oblong, about 40 mm wide, pinnatifid. Pinnules alternate on the pinnae rachis, arising at 45-60°, proximally fused to about half their length, free portion triangular to lanceolate, gradually pointed to obtuse apex, margin entire (fig. 1).

Leaf blade amphistomatic. Lower cuticle thin, its itercostal areas heavily papillate, cell outlines indistinct. Costal zones of elongate filed cells, nonpapillate. Stomata scattered in inter-

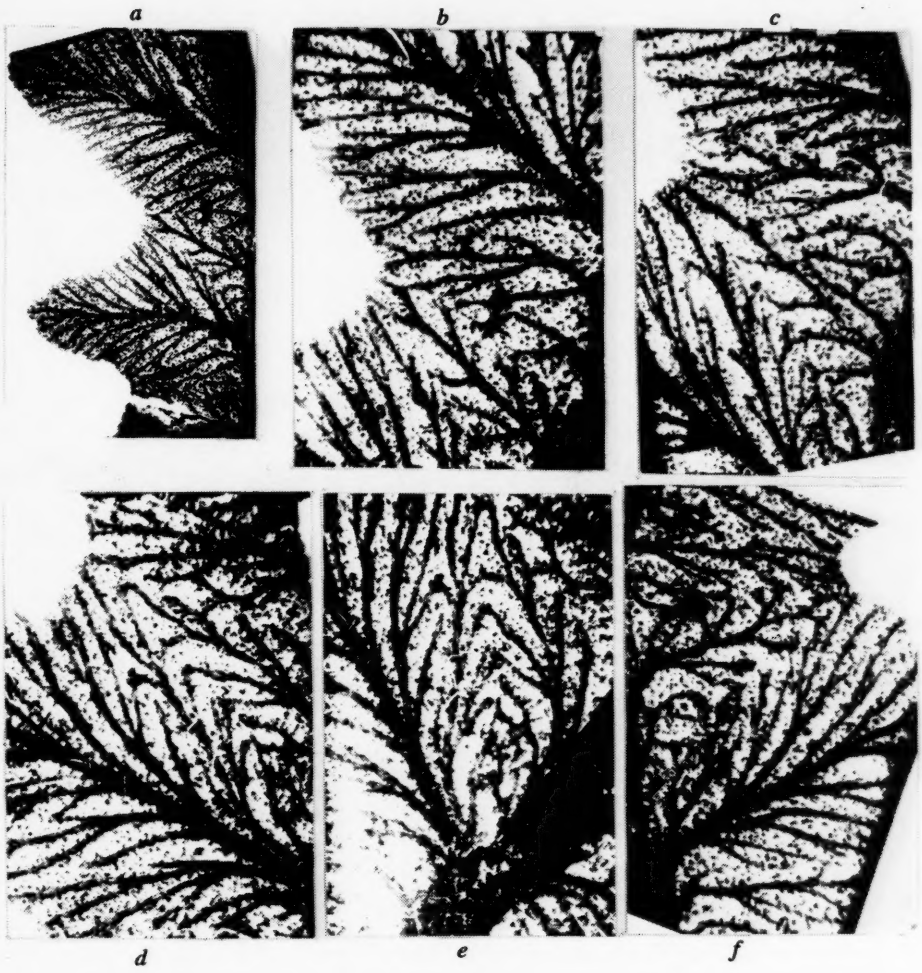

Fig. 3. *Scytophyllum vulgare*, interstitial pinnule region showing incipient reticulate venation: *a* - two proximally fused pinnules with interstitial pinnule incorporated in coherent part of blade, marked by pinnately branched "suture" vein, ×3; *b* - the same, enlarged to show venation of interstitial pinnule, its lateral veins approaching veins of adjacent normal pinnules, but typically not joining them, ×7; *c-e* - scalariform pattern formed by lateral veins of interstitial pinnule joining branches of acroscopic basal vein of adjacent normal pinnule. Note irregular meshes inside basal loop, ×7; *f* - interstitial pinnule venation with swollen ends of lateral veins, ×7.

costal zones, about 16-20 per 0.2 mm^2. Guard cells about 31-37 μm long, surrounded by 5 subsidiary cells with prominent papillae bulging over and occasionally closing stomatal pit (fig. 1). Encircling cells less prominently papillate, their number irregular. Occasional costal non-papillae stomata.

Upper cuticle moderately thick, showing distinct outlines of polygonal and rectangular cells about 52 × 31 μm with minute central papillae. Costal zones of somewhat longer cells less distinct than in lower epidermis. Stomata scattered, those close to costal zones tending to be parallel to their cell files. Stomatal frequency ranging from 5-6 to 9-13 per 0.2 mm^2. Contiguous stomata occurring sporadically. Guard cells about 31-43 μm long, surrounded by 5 to 6 subsidiary cells much smaller than rest, radially arranged, nonpapillate, thickened at stomatal pit border. Occasional subsidiary cells unspecialized, of normal size.

Venation

Venation of *Scytophyllum* was described as open, each pinnule showing a stout midrib with a number of repeatedly forking lateral branches. Laterals of the coherent pinnules ("pinnuloids") converge without actually joining each other. There can be a "suture" vein [4].

In *S. vulgare* the pinnule midribs are decurrent on the pinna rachis. Their lateral branches are catadromic, from 4 to 10 on each side (depending on the pinnule length), given off at acute angle, bent backwards, subopposite or alternate in catadromic pattern. They reach the margin at a concentration of about 15 terminal branches per 10 mm. Normally the laterals produce short blunt branches by unequal dichotomies and longer branches by equal or nearly equal dichotomies (fig. 2); the latter tend to be distal, but there can be short blunt branches above the first equal dichotomy as well. With several short side branches, the laterals appear bushy and even fasciculate. The basal pair of laterals ending in the sinus between pinnules are longer than the rest and more obviously fasciculate. The basal acroscopic laterals tend to be asymmetrically pinnate, producing short acroscopic and longer basiscopic branches, the latter being forked (fig. 3). Subbasal veins emerging from the decurrent part of the midrib are comparatively short, forking once or rarely twice. Occasional laterals are simple; they occur sporadically, and some reach only halfway to the margin.

In the free pinnules, distal branches of the laterals as well as their blunt side-branches typically approach each other without actually joining (fig. 2). Occasional veins form loops (unite after forking) or anastomose. In the coherent portions of the pinnae the situation is more complicated. These parts are supplied by the basal and subbasal laterals as well as by an interstitial "suture" vein. The latter runs parallel to the midribs of adjacent pinnules, reaching the sinus between their converging basal laterals, or not reaching it by a few millimeters; it is decurrent, giving off several pairs of short lateral branches which are simple or (proximal) once forked. Their ends are often thickened, as if glandular.

There is no evidence of this vein actually marking a suture between the coherent pinnules. It appears rather like pinnate venation of a small pinnule. Positionally, it can be a vestigial venation of an interstitial pinnule typically present in noncoherent peltasperm leaves.

Lateral branches of the interstitial ("suture") vein can be free, just approaching adjacent veins, or they tend to join branches of the basal laterals of adjacent pinnules forming angular

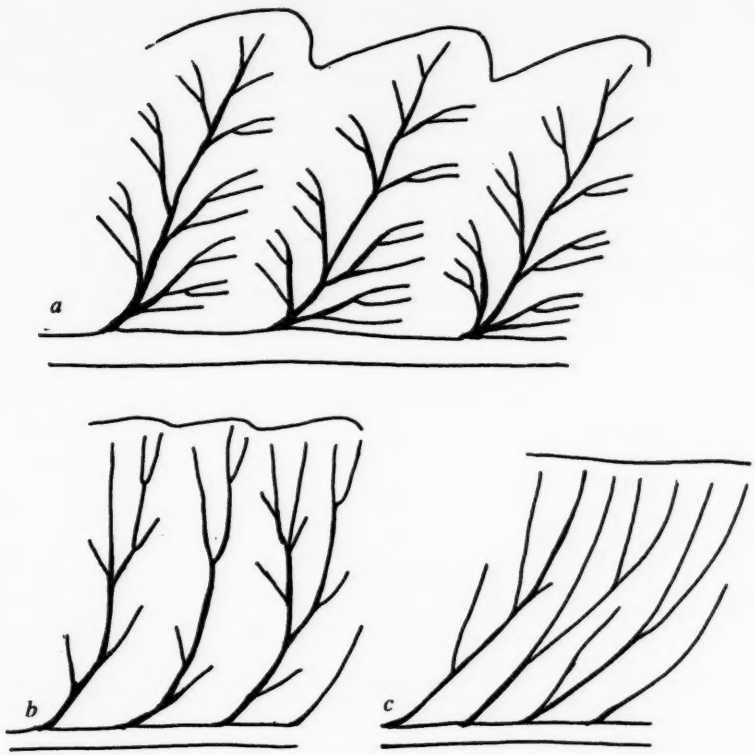

Fig. 4. Retroconvergence: *a* - coherent blade retaining cladophleboid venation of constituent pinnules; *b* - cladophleboid venation transformed by overtopping into fasciculate veins; *c* - further transformation of lateral veins resembling initial cladophleboid pattern.

areolae. Subbasal veins remain free within the proximal areolae or they loop between themselves or join lower branches of adjacent laterals. In figure 3 one distinct areole is formed by the proximal branches of the interstitial vein and the adjacent acroscopic basal vein. Free lower branches of these veins and the once-forked subbasal vein form an intricate irregular pattern within the areole. In another example, four subsequent branches of an interstitial vein form a series of joints with the adjacent acroscopic basal vein, while short subbasal veins are free, filling the lower areole. This pattern resembles scalariform tertiary venation of angiosperms.

To summarize, venation of the coherent portion tends to form irregular areolae and scalariform joints. Proximal areolae are filled with irregularly branching veins.

Interpretation of the Leaf Structure

Scytophyllum leaves have been described as "unicoherent," that is, processed through one round of segment fusion. However, their fasciculate proximal laterals suggest the composite nature of its pinnules though their constituent pinnuloids are scarcely evident. Distal laterals look much like normal cladophleboid dichotomous venation except that occasional blunt side-branches betray their origin from pinnate vein systems.

Since most peltasperms have cladophleboid venation with dichotomous laterals, we can surmise that, after marginal fusion, venation of the coherent pinnules as a whole converged on the original venation of their constituent pinnuloids. Vestigial features, such as fasciculate laterals or blunt side-branches, have been retained for undefinable evolutionary time, disappearing gradually in basipetal succession.

Proximal fusion of the pinnules could then actually manifest the second round of fusion on the way to the "bicoherent" leaf. Interstitial pinnules have lost their morphological identity already, but they are still marked by their vestigial venation — the interstitial ("suture") vein. Venation of the coherent blade shows a tendency toward a reticulate pattern but the vein fusions lag behind the marginal fusion of segments. These observations seem pertinent to the following morphological problems.

Retroconvergence

Compound organs evolved by integration of originally distinct structures that tend to resemble these constituent structures. Familiar examples are pseudanthia, inflorescences that look like flowers, or achenes that look like seeds. While there could be a strong adaptive component in these examples of retrograde convergence, the transformation of fasciculate vestigial veins of coherent pinnules into cladophleboid venation resembling that of their constituent pinnuloids seems adaptively meaningless. Whatever the genetic background of the organ fusion could be, the retroconvergent morphological trends seem to indicate gradual reversal of a modified genetic program to the original Gestalt inbuilt in the genomic memory. Such phenomena might reveal some little understood features of the genomic programming machinery.

Vascular Conservatism

The concept of vascular conservatism arose in connection with floral structures that supposedly evolved by fusion and reduction of their parts. According to this concept, evolution of vascular patterns lags behind other floral features, and while an organ can be obscured or even lost in fusion as a discrete morphological entity, its vascular bundles maintain their identity. The supposedly vestigial bundles have been widely used in morphological analysis, although several authors have presented strong arguments against vascular conservation [12].

The situation in *Scytophyllum* has some bearing on this much disputed issue. Here at least we have an undisputable example of vascular conservatism: leaf segments show various degrees of fusion while their vascular bundles normally do not fuse. And even when morphological boundaries are completely resolved in fusion, former segments can be recognized by their vestigial venation.

An explanation for conservatism in this case could be that the postgenital fusion is carried out by marginal meristems, while vascular bundles are initiated from derivatives of submarginal meristem at some distance from the margin. Incorporated in a compound organ, the former marginal meristems still repel vascular strands, thus preventing their union. Vascular conservatism then arises from the conservatism of marginal meristems. Subsequent modifications of the original venation pattern in *S. vulgare* by reduction of fascicles or by their reticulation show that vascular conservatism is transient, however.

Patterns of Leaf Development

During development, angiosperm leaves show both marginal and intercalary growth [7, 14]. The zone of marginal growth (marginal meristem s.l.) is divisible into the marginal initials (marginal meristem s.s.) which divide anticlinally, contributing to the adaxial and abaxial protoderms, and the submarginal initials which divide both anticlinally and periclinally, forming middle layers. The late meristem derivative of the submarginal meristem is characterized by the preponderance of anticlinal divisions, contributing to the leaf blade extension. Marginal growth is of comparatively short duration, while the cell division rates in the marginal meristem s.s. decrease earlier than in the submarginal meristem [6]. In contrast, fern leaves are formed by marginal growth only. Consequently, several authors have pointed out the lack of developmental homology between foliar organs of ferns and angiosperms [17].

Peltasperm leaves are fernlike, but their segments could be formed by fusion of subordinate units which could preserve their original venation. Vascular conservatism, as discussed above, might result from fusion by marginal initials which normally would not produce procambial strands. Incorporated in the coherent blade, the fused marginal meristems might retain their original developmental program, hence forming inner meristematic zones devoid of venation.

Subsequent transformations by reduction (retroconvergent cladophleboid pattern of unicoherent pinnules) or fusion (incipient reticulate pattern of bicoherent blades) might indicate corresponding changes in the developmental programs of the fusion meristems — either loss of function or acquirement of a new function.

The coherent blade of *Scytophyllum vulgare* is formed by the proximal parts of pinnules fused to the interstitial pinnules and to each other above the latter. Hence, it is traversed by a number of fusion meristems. Reticulate venation is initiated in this highly meristematic area, indicating a new function acquired by the fusion meristems, i.e., that of a plate meristem mediating vein fusions.

Perhaps pertinent to this hypothesis are observations [13] showing that, unlike other differentiated cells irreversibly committed into their respective developmental pathways, cells of fused tissues are capable of redifferentiation.

Conclusion

It is hypothesized that vascular conservatism (retention of original vein pattern in marginally fused leaf segments) in *Scytophyllum* and supposedly in other peltasperms and

gigantopterids with "coherent" leaves resulted from conservatism of the fusion meristems, maintaining their marginal features within the coherent leaf blade. Subsequently, the fusion meristems could be lost while venation of the coherent pinnules tended to converge on the original cladophleboid pattern of their constituent pinnupoids. This can be seen as a case of retroconvergence, a tendency of compound organs to resemble their constituent organs.

The incipient reticulate venation in the bicoherent pinnae of *Scytophyllum vulgare* contain a number of fusion meristems that could result from the latter changing their developmental program in the direction of plate meristem. Thus, both developmental complexity and reticulate venation of the typical angiosperm leaves might evolve in relation to the leaf coherence.

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NEW LATE ALBIAN ANGIOSPERMS FROM THE OKHOTSK-CHUKOTKAN VOLCANOGENIC BELT

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Abstract: Two new angiosperm genera, *Paratrochodendroides* and *Protoquereuxia*, are described from the Late Albian Inikchan beds in the southern part of the Okhotsk-Chukotkan volcanogenic belt.

Два новых рода покрытосеменных *Paratrochodendroides* и *Protoqueteuxia* описаны из верхнеальбских инканских слоев южной части Охотско-Чукотского вулканогенного пояса.

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Angiosperm leaves were collected from the 3000-5000 meter-thick volcanogenic deposits of the Ul'ya Basin in the southern part of the Okhotsk-Chukotkan volcanogenic belt (OCVB) in Okhotsk region, Khabarovsk Province. A continuous succession of Middle Cretaceous floral assemblages and their stratigraphic relations are present there in a single structural zone [18, 19].

Cretaceous mountainous floras from the OCVB differ from the lowland floras from the nonvolcanic deposits of this region. Differences between these floras are, first, the occurrence of the Early Cretaceous relicts *Phoenicopsis* and *Sphenobaiera* in the Late Cretaceous floras of the OCVB, and, second, the less important role of thermophyllic plants. The relicts persisted in the OCVB until the Campanian. That is why an Okhotsk-Chaun subprovince [19] within the Okhotsk-Chukotka Province, identified by V. A. Vakhrameev [26], is accepted. The composition and evolution of the Middle Cretaceous floras of the OVCB were studied previously [13, 18, 19, 20, 21].

The angiosperms described here were collected from two localities in the Late Albian Inikchan beds: (1) Inikchan Creek, Uenma River, where Inikchan flora underlies the beds with Amka flora, and (2) on the Ukundja River, left tributary of Ul'ya River.

Besides *Paratrochodendroides* and *Protoquereuxia* the type Inikchan locality contains the angiosperms *Dalembia* ex gr. *Vachrameevii* E. Lebed. et Herman, *Dalembia* sp., *Zizyphus* ex gr. *hyperborea* Heer, *Araliaephyllum* sp., *Ternstroemites* (?) sp., *Dicotylophyllum* sp. 1, *Dicotylophyllum* sp. 2, *Dicotylophyllum* sp. 3, and *Carpites* sp.

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The Inikchan floral assemblage is characterized by an association of the conifers *Metasequoia* with angiosperms *Paratrochodendroides, Menispermites*, and *Dalembia vachrameevii*. Unusual *Paratrochodendroides* and *Protoquereuxia* can be considered as ancestors of the true *Trochodendroides* and *Quereuxia* appearing higher in the section of the Amka beds. *Dalembia* ex gr. *vachrameevii* and *Menispermites* were not found there. These angiosperms are widespread higher in the section in the Cenomanian Grebenka floras. Probably this indirectly supports the hypothesis of the mountainous origin of the angiosperms that was suggested by Vakhrameev in 1947 [25].

Leaf impressions of *Paratrochodendroides* gen. nov. were collected in the type locality on the right bank of the Uenma River approximately 1 km downstream from the Inikchan Creek confluence. The plant-bearing layer was found by geologist V. V. Gromov in 1986. I collected flora from this locality in 1989-1990. Leaf impressions occur in a thin tuff layer, 1-2 mm thick.

Leaf impressions of *Protoquereuxia* were collected in the second locality on the left bank of the Ukundja River, approximately 1 km above its mouth.

The material is housed in the Geological Institute, Russian Academy of Sciences, Collection No. 3393. Drawings were made with camera-lucida [17].

Genus ***Paratrochodendroides*** E. Lebedev, gen. nov.

Name. From *para* (Latin) - similar, and *Trochodendroides* - name of the morphologically similar fossil genus.

Type species. *Paratrochodendroides gromovii* sp. nov.

Diagnosis. Leaves small or medium-sized, rounded-ovate, stalked, toothed, glandular. Leaf base slightly or deeply cordate. Apex tapered. Venation palmate, mixed craspedodromous-brochidodromous. Relatively thick basal veins diverging from petiole or slightly lower on leaf blade base. Inner pair of basals rising in distal part of leaf, external pair of basals bending outwards. Branches from basal veins either ending in teeth or joining in large loops.

Comparison. *Cercidiphyllum, Tetracentron, Trochodendroides*, and *Prototrochendroides*. The first two genera are extant with fossil representatives, the latter two are extinct. The main morphological characters of the leaf laminae of these genera are shown in table 1. These genera have similar mostly rounded-ovate, sometimes rounded-cordate leaves, toothed margins, and palmate venation with the inner basal veins extending into the distal part of the leaf.

Table 1 shows that these five genera fall into two groups. The first includes *Cercidiphyllum* and *Tetracentron*, and the second has fossil genera *Trochodendroides, Prototrochodendroides*, and *Paratrochodendroides*. The first group is characterized by palmate-brochidodromous (laciniate-brochidodromous) venation, but the fossil genera are characterized by mixed craspedodromous-brochidodromous venation.

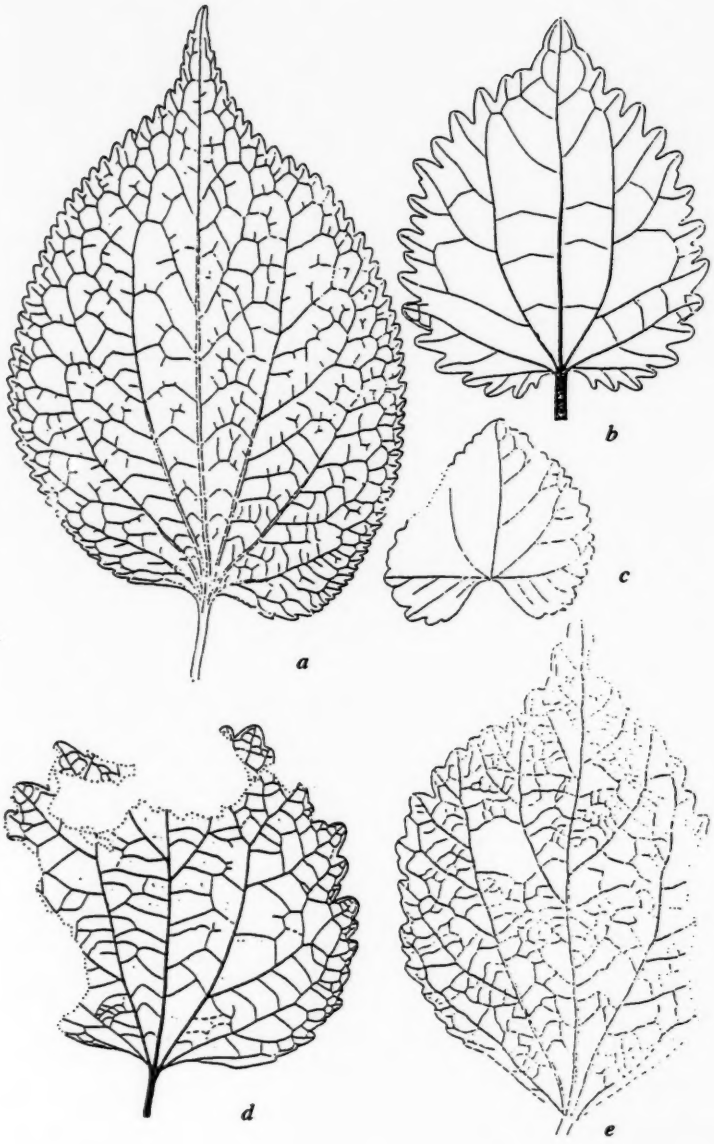
Paratrochendroides gen. nov. is similar to the extant genera of the first group in its cordate leaf base, and to *Tetracentron* in its tapered apex and origination of the basal veins from the petiole slightly lower on the leaf base.

Table 1

Leaf blade structure	*Cercidiphyllum*	*Tetracentron*	*Trochodendoides*	*Prototrochodendroides*	*Paratrochodendroides*
Form	Rounded-ovate	Rounded-ovate	From widely-rounded to ovate	Rounded, deeply cordate	Rounded-ovate
Base	From cordate to deeply cordate	Emarginate or cordate (rarely rounded-truncate)	Rounded-cuneate, truncate, weakly emarginate with cuneate decurrent petiole	From cordate to deeply cordate	From weakly to deeply cordate
Apex	Blunt, broad rounded (rarely sharp-pointed)	Tapered	Blunt or narrowed	Triangular-narrowed	Tapered
Margin	Toothed	Toothed	From toothed to lobelike-toothed	Toothed	Toothed (to deeply toothed)
Teeth	Appressed, apices displaced to anterior margin	Rounded-crenate	From rounded-crenate to trapezoid	Rounded	Trapezoid, lingulate
Venation	Palmate	Palmate	Palmate	Palmate	Palmate

Table 1, cont'd

Leaf blade structure	*Cercidiphyllum*	*Tetracentron*	*Trochodendroides*	*Prototrochodendroides*	*Paratrochodendroides*
Origination of basal veins	From leaf base slightly higher	From leaf base of slightly lower (from petiole)	From leaf base	From leaf base	From leaf base or slightly lower (from petiole)
Inner basal veins	Extending into distal part of leaf	Extending into distal part of leaf	Extending into distal part of leaf	Extending into distal part of leaf	Extending into distal part of leaf
External basal veins	Arise at 45° angle	Arise at 45° angle	Arise at 45° angle	Arise at 90° angle	Arise at 70-90° angle
Peripheral venation	Brochidodromous (laciniate-brochidodromous)	Brochidodromous (laciniate-brochidodromous)	Mixed craspedodromous-brochidodromous	Mixed craspedodromous-brochidodromous	Mixed craspedodromous-brochidodromous
Scalariform tertiary veins	Development	Predominant loops	Development	?	Development
Notes				Leaves small, cordate with thin basal veins	Leaves larger with thick basal veins


a
b
c
d
e

Paratrochodendroides is most similar to the fossil genus *Prototrochodendroides* [7] which was revised in [8]. These genera are similar in the open angle (up to 70-90°) between the midrib and lower basal veins. *Prototrochodendroides* leaves are small with broadly cordate base and thin basal veins. I. A. Iljinskaya [8] believed that *Prototrochodendroides* leaves may belong to grassy plants. V. A. Krassilov attributes *Prototrochodendroides* to *Ranunculales*.

Paratrochodendroides differs from *Prototrochodendroides* in larger leaves, thicker basal veins, and shape of marginal teeth—rather large trapezoid, rather than small rounded-crenate in *Prototrochodendroides*.

Similar genus *Trochodendroides* is widespread in the Cretaceous. The new genus differs from it primarily in the cordate, sometimes deeply cordate leaf base. It is important to note that the small teeth of *Paratrochodendroides* appear nearer to the petiole than those of *Trochodendroides* which has a truncate-rounded, general cuneate base. The lower basal veins of *Paratrochodendroides* diverge at a wider angle (70-90°) than those of *Trochodendroides*. Craspedodromous venation is more characteristic for the lower part of *Paratrochodendroides* leaves, while it is more characteristic for the upper part of *Trochodendroides* leaves. For example, *Trochodendroides bidentate* Vassil. et Golovn. has well-developed craspedodromous venation in the upper part of leaves and brochidodromous branches of lower basal veins.

Figure 1 shows a reconstruction of *Paratrochodendriodes* and of some *Trochodendroides*, *Prototrochodendroides* and *Tetracentron* that demonstrate these differences. Among the extant genera, *Paratrochodendroides* is nearer to *Tetracentron* than to *Cercidiphyllum*. Fruits identified as *Carpites* sp. were found in the type locality with numerous *Paratrochodendroides* leaves.

Remarks. There are different interpretations about the composition of *Trochodendroides*. Some authors recognized several species of *Trochodendroides* from the Amur Basin, while others united them in *Trochodendroides arctica* [11, 16]. These differences are related to the polymorphism of *Trochodendroides* leaves, and show the necessity for revision of this genus.

Paratrochodendroides gromovii E. Lebedev, sp. nov.

Pl. I, figs. 1-5

Name. In honor of geologist V. V. Gromov.

Holotype. Geological Institute, No. 3393/326-7; Okhotsk region of Khabarovsk Province, Inikchan beds, Amka series, Late Albian.

Fig. 1. Comparison of *Paratrochodendroides* gen. nov., with morphologically similar genera: *a* - *Tetracentron sinensis* Oliv., extant [19, fig. 19]; *b* - *Paratrochodendroides gromovii* E. Lebed., gen. et sp. nov., reconstruction (×1); *c* - *Prototrochodendroides jacutica* Budants. et Kiritchk. (×3) [6, fig. 64.3]; *d* - *Trochodendroides notabilis* Herman (×1) [4, fig. 36]; *e* - *Trochodendroides vassilenkoi* Iljinskaya et Romanova, holotype (×1) [6, fig. 75.1].

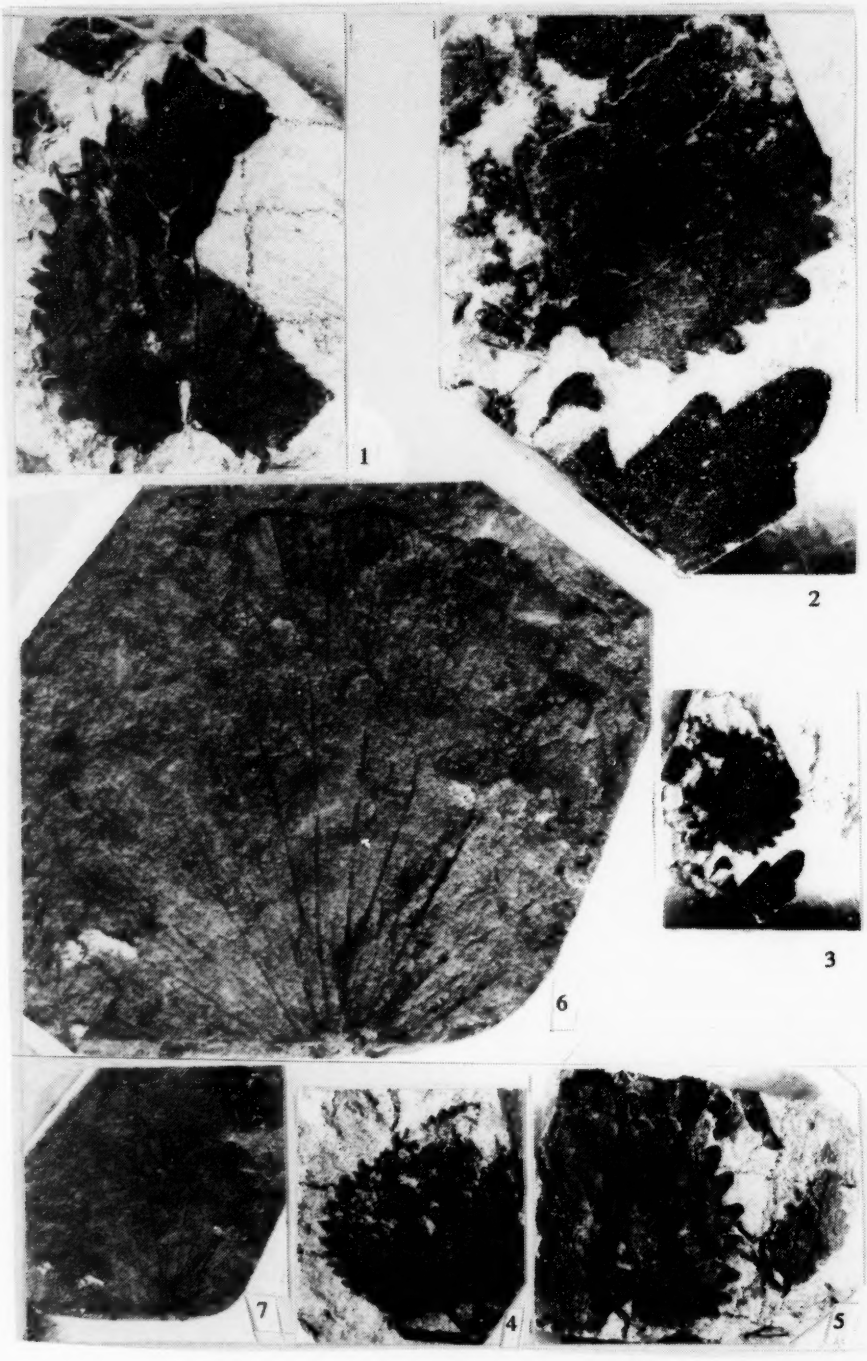


PLATE I

Description (fig. 2*a-j*). Leaves are medium sized or small, rounded-ovate, stalked, dentate or bidentate, glandular, typically 30×15 mm to 60×30 mm. Judging by the fragment of the leaf base (fig. 2*d*), leaves may reach up to 100-120×50-60 mm. Leaf base from weakly to deeply cordate, rarely almost truncate (fig. 2*a-j*). Margin is dentate or bidentate. Teeth are trapezoid, ligulate, rounded, or rarely triangular-trapezoid. Teeth appear in base near petiole (fig. 2*f, g*), their size increasing toward the middle part of leaf. Near apex they are rounded-appressed (fig. 2*b, g*). Palmate venation usually five-veined, mixed craspedodromous-brochidodromous. Basal veins are relatively thick, especially in small leaves. Inner basal veins round parallel to the midrib into distal part of leaf, where they disintegrate and join midrib branches. External basal veins and their branches usually end in teeth (fig. 2*a-e*). Basals diverge from apex of petiole as if splitting it, or slightly lower on base (fig. 2*i*). Some veins end in teeth and others join near leaf margin in large angular loops while their branches end in teeth. Craspedodromous venation is more typically developed in lower part of leaf. Lateral veins are curved or almost straight (fig. 2*a-f*). Thin marginal veins are observed in teeth (fig. 2*h*), and have short thin ramifications which disappear near leaf margin. Scalariform tertiary veins diverge from basal and lateral veins (fig. 2*a-j*).

Remarks. Some leaf fragments have more developed basal veins. It is not clear whether they are related to *P. gromovii* or represent a new species of this genus.

Material. More than 30 differently preserved leaf fragments from the type locality.

Genus ***Protoquereuxia*** E. Lebedev, gen. nov.

Name. From *proto* (Greek) - first, and *Quereuxia* - name of the morphologically similar fossil genus.

Type species. *Protoquereuxia uljensis* sp. nov.

Diagnosis. Leaves rounded, peltate; margin toothed broadly, or gently sinuate. Venation dichotomous-radiate, reticulate with anastomoses and distinct marginal vein. Main veins ending in teeth. In upper part of main veins, apical fascicles of lateral veins formed, curving and merging with each other and with veins of adjacent fascicles. External and uppermost lateral veins in these fascicles merged with marginal vein.

KEY TO PLATE I

In all cases, except where marked, size is natural.

Figs. 1-5. *Paratrochodendroides gromovii* E. Lebed., sp. nov.: 1 - holotype, No. 3393/326-7; 2, 3 - fragment of medium-sized leaf and deeply incised part of margin lower part No. 3393/326-12; 2 - ×3; 4 - slightly deformed leaf with marginal glands, No. 3393/326-6; 5 - medium-sized leaf with small teeth (left), and small leaf (right), No. 3393/326-2b.

Figs. 6, 7. *Protoquereuxia uljensis* E. Lebed., sp. nov., holotype No. 3393/333-1a, 6 - ×3.

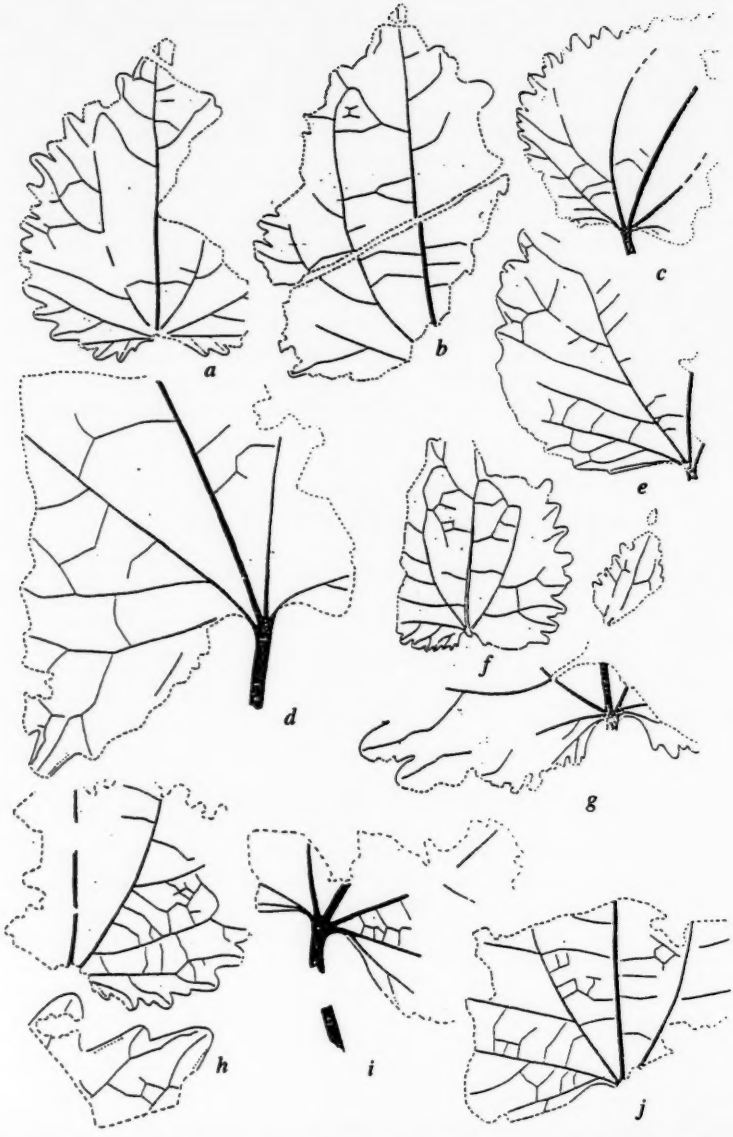


Fig. 2. *Paratrochodendroides gromovii* E. Lebed., sp. nov.; *a* - almost complete leaf, holotype, spec. 3393/326-7 (×1); *b* - incomplete leaf, spec. 3393/326-25(×1.1); *c* - slightly deformed leaf with marginal glands, spec. 3393/326-6(×1); *d* - fragment of deeply cordate base of large leaf, spec. 3393/326-5(×1.5); *e* - leaf with almost straight lateral veins, spec. 3393/326-4(×1); *f* - medium-sized leaf with small teeth (left) and small leaf (right), spec. 3393/326-2b(×1); *g* - fragment of leaf base showing increase in size of teeth, spec. 3393/326-25(×1); *h* - fragment of medium-sized leaf and deeply incised part of margin (lower), spec. 3393/326-12(×1.5); *i* - basal veins moved from petiole, spec. 3393/326-10(×1.2); *j* - lower part of leaf, spec. 3393/326-11(×1.2).

Comparison. The morphologically similar genus *Quereuxia* was erected by A. N. Kryshtofovich [14] in 1953 with the type species, *Neuropteris angulata* Newb. [9], from the Cretaceous of North America. Leaves of this type were described under several names [1, 10, 12, 14, 21] and others. Similar leaves are widespread in the Cretaceous of northeast Asia. V. A. Samylina [24] suggested that this aquatic plant has rosettes of floating leaves and whorls of finely divided submerged leaves. Samylina characterized floating leaves of this plant [24, p. 99]: "margins of leaflets are serrate or crenate-toothed or emarginate... Venation is imperfect-pinnate with more or less distinct midrib, from which fan-shaped secondary veins depart under sharp angle. Other veins merge with thin marginal vein." She stated that this character is seen only when a specimen is very well preserved; Bell. earlier, had noted this character. Kryshtofovich [14, p. 24] wrote that "leaflet venation is radiate or almost pinnate with more or less distinct midrib from which lateral springs pass under angle 20° and more. Lateral springs are craspedodromous, dichotomous and join by anastomosis." Later this character of the genus *Quereuxia* was reprinted in [1]. Therefore, the new genus *Protoquereuxia* differs from *Quereuxia* in the presence of apical fascicles of lateral veins which are completely merged with each other and with the marginal vein.

However, there is some resemblance between *Protoquereuxia* and *Quereuxia* in the peripheral venation. Thus the leaflet type of *Quereuxia* [15, 16], illustrated here in fig. 3*e*, shows that *Quereuxia* also has the apical system of lateral veins, which sometimes join each other, but this resemblance is not sufficient for uniting the two species (fig. 3*a-e*). For the final resolution of this question it is necessary to study the material from the type locality in North America [9].

Quereuxia leaves with both pennate and radiate venation are known, for example, *Q. striata* [22] and *Q. rotundifolia* [8]. The relation of these leaves to *Quereuxia* and *Protoquereuxia* needs to be suited in future. It should be noted that compound leaves and rosettes of *Protoquereuxia* are unknown.

A similar genus is *Jonqueria*, erected by V. A. Krassilov from the Senonian of Sakhalin [12, p. 109], who wrote in the *Jonqueria* diagnosis that "two veins enter the marginal serrations joining at the marginal gland." Therefore, *Protoquereuxia* differs from *Jonqueria* in the presence of apical fascicles of lateral veins.

Protoquereuxia uljensis E. Lebedev, sp. nov.

Pl. 1, figs. 6, 7

Name. From the Ulja River.

Holotype. Geological Institute, No. 3393/333-1a; Okhotsk region of Khabarovsk Province, Ukundja River, Inikchan beds, Amka series, Late Albian.

Description (fig. 3*a-d*). Leaves (leaflets?) are rounded, peltate, margin is toothed, broadly or gently sinuate, up to 30 mm in size. Venation is dichotomous-radiate, reticulate, with anastomosis and distinct marginal vein. Main veins go out from point of fastening which is near lower margin (fig. 3*d*), then they ramify dichotomously, join by anastomoses and end in teeth (fig. 3*a-c*). Original fascicles of lateral veins are in apical part of main veins (fig. 3*a-c*). Thin veins where seen, form network of long relatively large loops which are oriented along main veins (fig. 3*a*). Apical fascicles are formed by curved lateral veins, from which inner lateral veins are curved

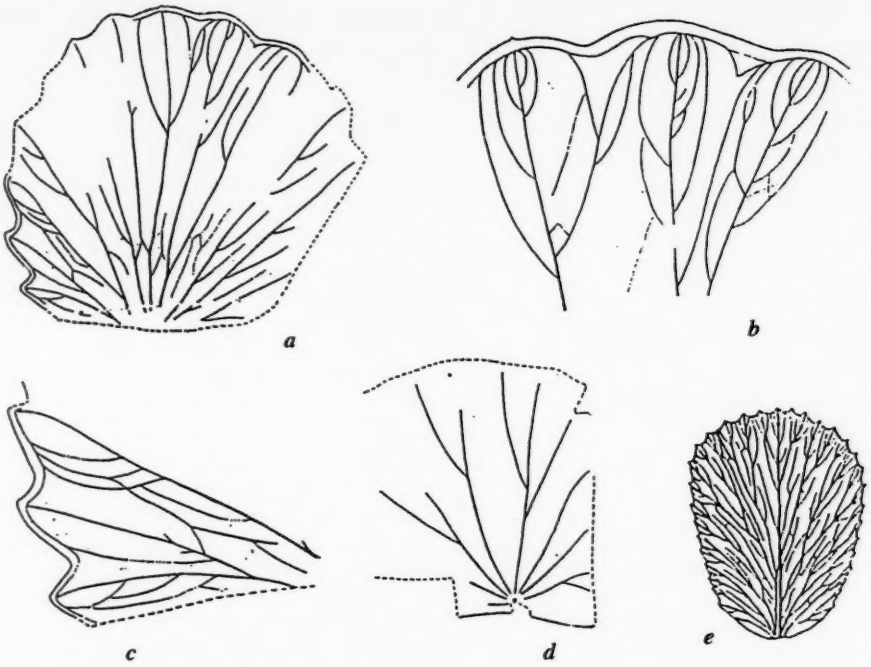


Fig. 3. *Protoquereuxia uljensis* E. Lebed., sp. nov., and comparison with morphologically similar genus *Quereuxia*: *a-c* - *Protoquereuxia uljensis* E. Lebed., sp. nov., holotype, spec. 3393/333-1a; *a* - (×1); *b*, *c* - details of peripheral venation (×1.6); *d* - characteristic of the moved veins in leaf base, spec. 3393/333-3(×1.2); *e* - *Quereuxia angulata* (Newb.) Krysht. [11, fig. 3].

and successively merged with each other, forming closed loops along main veins. External and upper lateral veins approach teeth, where they are curved and successively merge with marginal vein. The uppermost lateral veins of fascicles pass to apex of the main vein (fig. 3*b*, *c*), and external lateral veins merge with veins of adjacent fascicles. In this case the close lengthened loop is observed, which is formed by the splitting and then merging of the same vein (fig. 3*b*).

Remarks. Midribs are absent in leaves of the collection. Incomplete preservation of the material did not allow study of details of the structure of the apical fascicles or show the thinner veins which form the network of the little loops between lateral veins.

Material. Four leaves and two casts from one locality.

In conclusion, I note that the diversity of the angiosperms from the type locality of the Inikchan flora is underestimated. For example, the leaf fragment that was considered to *Termstroemites* most probably belongs to a new genus, etc.

I express my deep gratitude to Professors M. A. Akhmetiev and V. A. Krassilov, geologist V. V. Gromov, and others who helped in this research.

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NEW HAMAMELID FRUTIFICATION FROM THE PALEOGENE OF KAMCHATKA, WITH COMMENTS ON *Trochodendrocarpus* AND *Nordenskioldia*

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Abstract. *Itelantha*, a new genus of spicate inflorescence-bearing flowers with bicarpellate gynoecia and small distinct sepals is described from the uppermost Paleocene-Lower Eocene of northwestern Kamchatka. It enlarges the diversity of Paleocene hamamelidaceans represented by the dominant *Nyssidium-Trochodendrocarpus* group. *Nordenskioldia*, another widespread genus, may represent a separate family related to magnoliids or hamamelids.

Новый род *Itelantha* описан по соплодием отношений верхнего палеоцена – нижнего эоцена Камчатки. Плоды развивались из бикарпеллятного гинецея с остающимися листочками околоцветника. Этот род дополняет разнообразие палеогеновых гамамелид, представленных также доминирующей группой *Nyssidium – Trochodendrocarpus*. Другой широко распространенный род *Nordenskioldia* представляет самостоятельное семейство, близкое к магнолиевым и гамамелиевым.

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Introduction

Hamamelidaceae is phylogenetically important as a core family of Hamamelidales, a major order of angiosperms. Until recently, next to nothing was known of the early history of this family, although Platanaceae, a related family, has an extensive fossil record. Presently, the geological history of hamamelidaceans is traced to the Early Cretaceous [5, 7]. It appears, however, that the Paleocene was the acme for the lower hamamelids. Major Eurasian and North American plant localities of this age contain abundant fructifications that have been compared to *Nyssa* or *Cercidiphyllum* [1, 8]. Krassilov [10, 11] has described some of them as paniculate infructescences with paired proximally fused follicles, thus assignable to Hamamelidaceae and for the first time emerging as a dominant plant group. We will comment on some controversial opinions about this and related groups of Paleocene plants.

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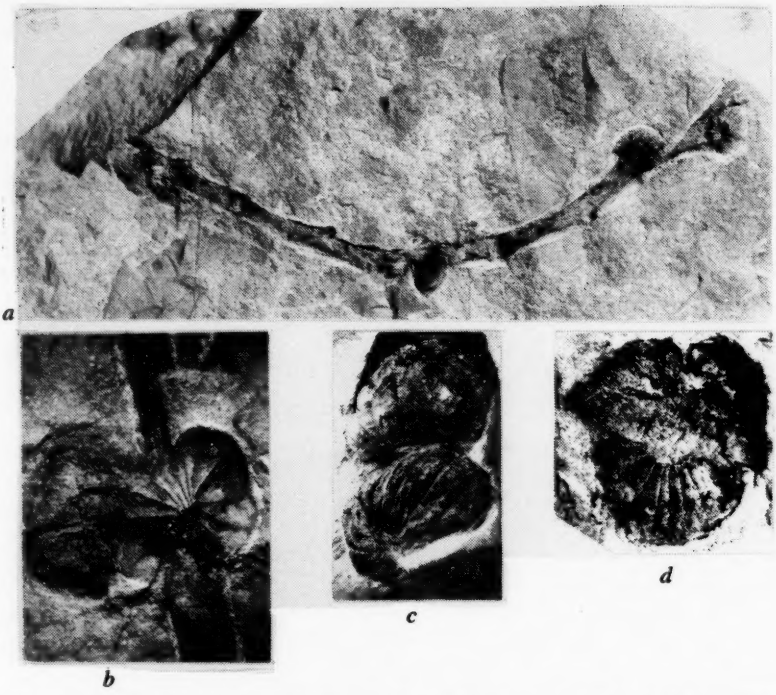


Fig. 1. *Nordenskioldia borealis* Heer: *a* - fruiting twig, ×1; *b* - fruit emerging from its calyptra which remains attached to axis, ×5; *c* - fruit (top) preserved alongside the open calyptra, ×5; *d* - open calyptra still containing fruit, ×5.

Trochodendrocarpus Kryshtofovich

Type species. *Trochodendrocarpus arcticus* Kryshtofovich, 1958 [13].

Neotype. No. 563-221, Krassilov [1], p. 60, pl. XXI, fig. 1, Tsagajan locality near mouth of Bureya River, Lower Paleocene.

Comments. Kryshtofovich [13] has identified this species as "*Nyssa*" *arctica* Heer [8]. While it has been shown that *Nyssidium arcticum* is generically, or at least specifically distinct from *Trochodendrocarpus* [2], the latter must be assigned to a different species for which the name *Trochodendrocarpus arcticus* can be validated by retypification. Since Kryshtofovich's collection is lost, a neotype has been selected from the Tsagajan collection described in [11]. Crane [2] has interpreted *Trochodendrocarpus* as a leafy twig bearing racemose fructifications rather than panicles. However, all the specimens from the Tsagajan locality, and there are several dozens of them, are branched infructescences which obviously have been shed as a unit. There are no definite leaf scars and the side branches diverge at regular intervals and angles. Therefore, the original interpretation of *Trochodendrocarpus* as a large (about 50 cm long) panicle

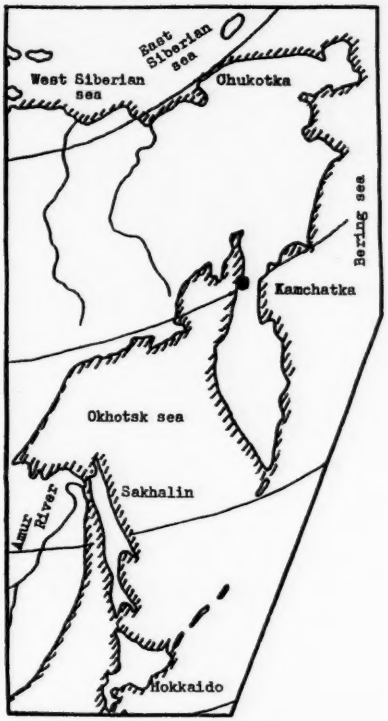


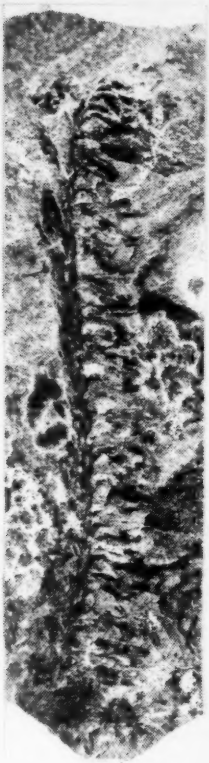
Fig. 2. Locality of *Itelantha densiflora* gen. et sp. nov.

is retained here. The plant might have been a small tree producing a few such panicles high in the crown, like extant aralias.

As for the supposed relationship of the *Trochodendrocarpus-Nyssidium* group to *Cercidiphyllum*, a single genus of Cercidiphyllaceae currently in the order Trochodendrales, we could not find any reliable evidence of phylogenetic continuity. *Cercidiphyllum* have pseudanthia of four, perhaps originally decussate, flowers consisting of a single abaxially dehiscent follicle subtended by a bract. To produce such a structure from *Trochodendrocarpus* or *Nyssidium*, the panicle or raceme has to be reduced to a single flower, one carpel of the syncarpous pair has to be lost, and the dehiscent suture has to be reversed [2].

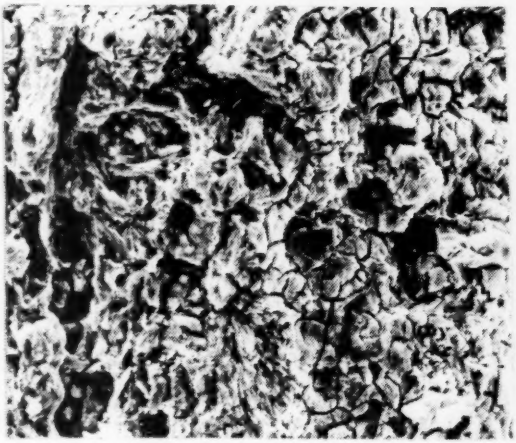
However, *Trochodendrocarpus*-type morphology has remained fairly constant for about 50 mln years, while the unmistakable *Cercidiphyllum* pseudanthia appeared in the Miocene some 40 mln years after the time of vigorous dispersion and diversification of the *Nyssidium-Trochodendrocarpus* group.

It seems more parsimonious to derive *Cercidiphyllum* from the early ranunculids, such



a

b



c

d

as *Caspiocarpus* with apocarpous abaxially dehiscent follicles [12]. The Trochodendrales might then be conceived of as true "woody Ranales," that is, sister group of ranunculids in which the woody habit is derived. However, this remains an open question.

Nordenskioldia Heer

Type species. *Nordenskioldia borealis* Heer [9], p. 65, pl. 11, figs. 1-13, Paleocene of Spitsbergen, revised in [4], p. 1314, figs. 2-4.

Comments. *Nordenskioldia* includes the easily recognizable fruit remains known from each of the larger Paleocene plant localities in northern Eurasia and North America. The fruits consist of about 20 fruitlets arranged in a single circle on the apically protruding receptacle. The fruitlets are laterally connate at the ovary level, with the persistent free short reflexed styles, separable when ripe, with a single seed.

These fruits are borne singly or in pairs on very long axes that have been found in the Amur Province, Mongolian and North American localities [3, 4, 14, 15]. Some infructescences are bearing umbrella-like structures from which the fruits have fallen.

Crane et al. [3, 4] and Manchester et al. [15] have supported an earlier suggestion of trochodendracean affinity [13], although the inflorescence morphology (loosely spicate in *Nordenskioldia* vs. cymose in *Trochodendron*), fruit type (follicetum vs. septicidal capsule), and seeds are entirely different. The interpretation of umbrella-like structures as exocarps [4] is rather questionable, the more so that in the Tsagajan (Amur Province) material these structures are bivalvate and calyptrate, spreading umbrella-like after the fruits are shed (fig. 2).

Moreover, there is some evidence from buds and incompletely preserved flowers that *Nordenskioldia* had heterochlamydeous perianths (fig. 1). In the latter case the caliptrate umbrellas could be formed of connate tepals, as in Magnoliaceae and some Hamamelidaceae.

Other families with similar gynoecial structures are Illiciaceae, with apically protruding receptacles and radially spreading one-seeded follicles, and Menispermaceae, with whorled apocarpous carpels and closely comparable leaf morphology, but distinct in the seed characters. We feel that *Nordenskioldia* represents a separate extinct family (Nordenskioldiaceae), perhaps related to magnoliids or hamamelids.

Itelantha Krassilov et Fotyanova, gen. nov.

Name. After Itelmen, indigenous people of Kamchatka, and *anthos* - flower.

Fig. 3. *Itelantha densiflora* gen. et sp. nov.: *a* - fruiting axis, holotype No. 487-23, ×1.3; *b* - part of same, showing bracts and tepals at base of three distal flowers, ×8; *c, d* - stomata on impression of follicle, SEM, ×500 and ×700.

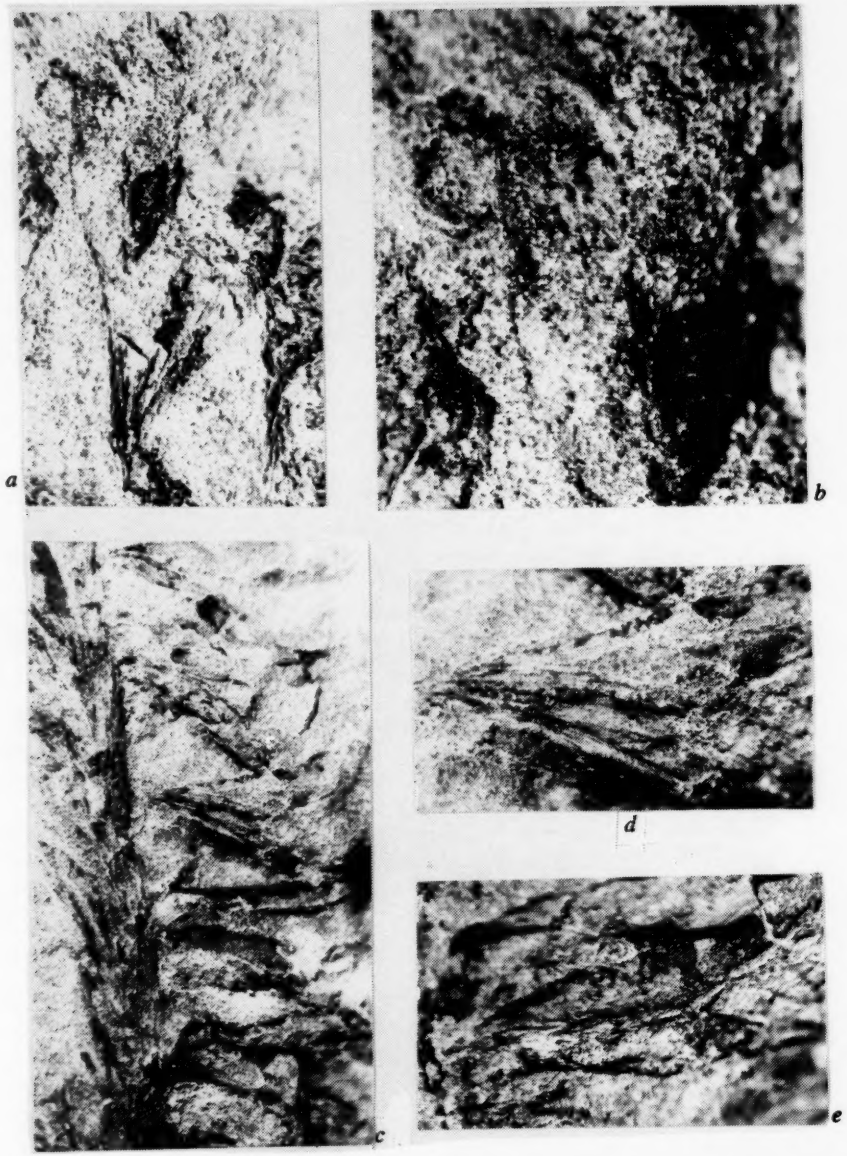


Fig. 4. ***Itelantha densiflora*** **gen. et sp. nov.:** ***a*** **- paired follicles with seed at distal end of left follicle, ×9;** ***b*** **- seed magnified, ×20;** ***c*** **- part of fruiting axis, ×5;** ***d*** **- paired follicles, ×9;** ***e*** **- split follicle, ×9.**

Type species. *Itelantha densiflora* Krassilov et Fotyanova, sp. nov., northwestern Kamchatka, Late Paleocene-Early Eocene.

Diagnosis. Dense spike of unisexual flowers in axils of small bracts. Perianth of small tepals adnate to base of ovary, persistent at fruit. Gynoecium of two proximally fused, distally diverging carpels developing into adaxially dehiscent follicles. Seeds several to many per locule, narrowly winged in median plane, slightly notched at micropylar end.

Itelantha densiflora Krassilov et Fotyanova sp. nov.

Figs. 3-5

Name. From *densus* (L.) - dense, and *floris* (L.) - flower.

Holotype. Coll. 3736, No. 4/87-23, Paleontological Institute, Moscow, Evrava-veyem River, northwestern Kamchatka, Upper Paleocene - Lower Eocene.

Locality. The fruiting axis came from the Upper Paleocene Tkaprovayam Formation of conglomerates and sandstones with shale interbeds, cropping out along the Evrava-veyem River, northwestern Kamchatka. This locality occurs 1.5 km upstream of the mouth of its tributary, Kupol Creek. It was found in 1987 by Fotyanova who preliminarily identified leaf remains of *Magnolia* sp., *Trochodendroides arctica* (Heer) Berry, *Platanus* sp., *Alnus beringiana* Budants., *Populus* sp., *Nyssa budantsevii* Fotyanova, *Ambroma* sp., *Cornophyllum svidiiformis* Budants., *Aesculus magnificum* (Newb.) Iljinsk., *Rhus* sp., *Leguminosites* sp. (pod), "*Cordia*" *kamchatica* Cheleb., *Ceanothus* sp. and *Peculnea* sp.

This floristic assemblage dominated by *Nyssa* and *Ambroma* is thought to be stratigraphic-

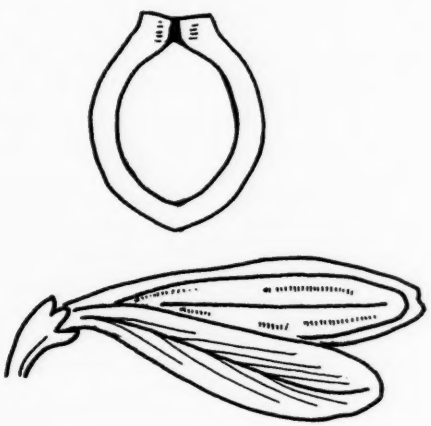


Fig. 5. *Itelantha densiflora* gen. et sp. nov., paired follicles and seed.

cally equivalent to the coastal Chemurnaut locality assigned to the Upper Paleocene-Lower Eocene by Sevora, Fotyanova and Fradkina [16].

Description. A single specimen is an impression of an incomplete fruiting axis preserved on a gray shale slab. The axis is 70 mm long, 1 mm thick, bearing ca. 38 flowers at fruiting stage. Most of the flowers are on one side of the axis (to the right in fig. 3) while those on the other side are buried in the rock, typically showing one of the follicles. This arrangement suggests that the flowers were originally borne in two rows in a one-sided spike or raceme. They are about 2 mm apart, practically sessile, although with a very short decurrent stalk. A small bract less than 1 mm long is discernible in most flowers, while the minute tepals at the base of the gynoecium are seen in a few flowers only.

No more than two sepals are seen on the impression, suggesting four as their most probable number. The sepals are free, rounded-triangular, adaxially slightly convex. No stamen scars are discernible.

The gynoecium consists of two carpels proximally fused about 1/3 of their length, then diverging at acute angle. The carpels are about 18 mm long, dehiscent along the adaxial suture (facing away from the subtending bract), abaxially showing a prominent keel from which thin but distinct striation spreads at acute angle, distally stretching almost parallel to the keel. The apices of the follicles are rounded or slightly notched, lacking any remains of stigmatic structures. Some follicles are variously bent or folded, their impressions appearing not to be woody structures.

Impression fragments mounted for SEM occasionally show outlines of sinuate cell walls, as well as rather dense stomata, some contiguous, variously oriented, with guard cells sunken in rounded stomatal pits surrounded by no less than six radially disposed subsidiary cells.

No seeds have been observed within the locules. However, three seeds are preserved at the tips of three different follicles. These seeds are ovate, slightly pointed at chalazal end, truncate and slightly notched at the micropylar end, 1.1 mm long with a central body about 2/3 of their length.

Comparison. This fruiting axis shows a typical hamamelidacean gynoecial structure of two proximally united, distally free carpels developing in follicular fruits. Spicate inflorescences and much reduced tepals are also common in the Hamamelidaceae. The seed size suggests many, or at least several, ovules per locule, which is less common in the latter family. The position of a few preserved seeds protruding from the follicles agrees with a dispersal mechanism by which the seeds are squirted out from the locule by the pressure of contracting fruit walls, as in *Hamamelis* [17]. The Kamchatkan fossil is obviously different form the recently described Cretaceous hamamelidacean flowers which are epigynous or semiepigynous with hypanthial perianths [5, 7]. These flowers are either longly stalked, perhaps solitary, or borne in compact heads.

The more readily comparable group is *Nyssidium-Joffrea-Trochodendrocarpus* from Paleocene and younger deposits of Eurasia and North America. At least in *Trochodendrocarpus*, but perhaps also in other genera of the group, the gynoecia consist of two proximally fused carpels which are externally similar to those of *Itelantha*. However, in the *Nyssidium* group, flowers are borne in loose racemes or panicles rather than dense spikes and they are distinctly stalked. Furthermore, they do not show persistent tepals and their seeds have a well-developed one-sided wing.

The dense spicate inflorescence of *Itelantha* suggests a pollination vector different from both *Archamamelis* (which could be beetle-pollinated like the majority of epigynous flowers) and the loosely racemose or paniculate and supposedly wind-pollinated *Nyssidium*-group.

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A PALEOGENE CONIFER WITH MEGASTROBILAR "INFLORESCENCES" FROM MONGOLIA

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Abstract. *Gobiostrobus* from the Upper Paleocene Naran-Bulak Formation of the South Gobi is unusual in having its megastrobili borne in the axils of bracts on fertile inflorescence-like shoots. The cone and leaf morphologies suggest a taxodiacean affinity of this unique conifer.

Gobiostrobus из верхнего палеоцена свиты Наранбулак, Южный Гоби, отличается собраниями мегастробилов в пазухах брактей на фертильном побеге. По признакам стробилов и листьев этот род отнесен к таксодиевым.

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The Naran-Bulak locality in the Nemegt Depression, South Gobi, contains a rich assemblage of Late Paleocene plants dominated by *Trochodendroides* and an unusual conifer assigned to a new genus of Taxodiaceae [3]. Subsequent SEM studies have revealed some additional anatomical characters, making it necessary to emend the diagnosis and extend taxonomic comparisons as well as evolutionary implications.

Gobiostrobus Makulbekov, nom. nov.

Pl. I, figs. 1-6; Pl. II, figs. 1-5; Pl. III, figs. 1, 2; Pl. IV, figs. 1, 2

Name. From Gobi Desert, and *strobus* (L.) - cone; here introduced for the preoccupied *Gobia* Makulbekov [3] non *Gobia* Reinke, 1889 (Algae).

Type species. *Gobiostrobus mongolica* (Makulbekov) Makulbekov [3], Upper Paleocene Naran-Bulak Formation, Naran-Bulak and Tsagan-Khushu, South Gobi.

Emended diagnosis. Heterophyllous conifer with ultimate branchlets ca. 80-100 mm long, with thin axis. Leaves on ultimate branchlets bifacial, linear-oblanceolate, pointed, spirally arranged, decurrent, free portion ca. 15 mm long, spreading at acute angle. Proximal leaves shorter, spreading at a more open angle. Stomata in two bands, scattered, irregularly oriented, anomocytic, monocyclic.

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Penultimate shoots with subulate scale-leaves. Fertile penultimate shoots bearing megastrobili laterally in axils of each scale-leaf, terminating in subapical cone or occasionally proliferating in leafy shoot with leaves as in ultimate branchlets.

Megastrobili spirally attached, ca. 10 per fertile zone 80 mm long, typically 5 mm apart on one side of axis, derived at acute angle, shortly stalked or almost sessile. Stalks ca. 2 mm long, terete, longitudinally striated, basally adnate to subtending leaf.

Megastrobili globose, ca. 12 mm in diameter, compact, consisting of about 6 to 8 (exact number not defined) cone scales. Cone axis not thicker than stalk. Cone scales subopposite, distally appressed to each other, attached at acute angle, peltate, consisting of slender stalk distally expanded in rhombic shield ("escutcheon") ca. 7 mm across in middle part of cone, proximal and distal scales somewhat smaller. Shields divided by median groove into equal halves, with central umbel and radial striation, shield margins slightly recurved. Shield epidermis with scattered stomata. Hypodermal tissue with thick fibers extending along scale stalk and radially diverging in shield. Vascular strand entering cone scale dividing in scale stalk into two equal arms, further repeatedly dividing in shield to form two series of apically thickened terminal bundles.

Seeds small, erect, attached near shield margin, symmetrically winged in median plane, with protuding micropyle.

Remarks. This conifer is abundantly represented by fertile shoots bearing small globose megastrobili in the axils of scale leaves. Obviously, this is the characteristic fashion in which the seed cones have been borne. Two fertile shoots apically proliferate in vegetative shoots (pl. I, fig. 1) identical in the leaf characters to the associated ultimate branchlets, which have been recognized as belonging to the same plant. The cones are typically preserved as impressions, showing outlines of rhombic scales. However, a few cones are split longitudinally showing axis and scale stalks (pl. II, fig. 3). Moreover, the impressions are covered with a yellow film of ferric oxides which, when seen under the SEM, revealed epidermal cells and stomata. Evidently the ferriferous mineralizing fluids have been impregnated, subcutaneously imprinting the inner surface of the cuticle. In the split cones the hypodermal fibers and vascular strands are partly preserved as ferric incrustations (pl. II).

Seeds were seen in only a few cones. More commonly, they are concealed by the recurved margins of the scales. They seem to have been borne in a single row of no less than four seeds, but their exact number was not determined.

Comparison. Leafy shoots resemble *Taxodium* and *Glyptostrobus* while megastrobili with distinctly peltate cone scales (bract-seed scale complexes) are comparable with a number of extant and fossil genera of Taxodiaceae and Cupressaceae; the latter differ, however, in the verticillate arrangement of their leaves and cone scales. Erect ovules restrict comparisons to *Taxodium* (other taxodiaceans with erect ovules, i.e., *Glyptostrobus* and *Cryptmeria* have nonpeltate cone scales) in which, however, the bract is smaller than the seed scale; their equal development in *Gobiostrobus* is like in the *Sequoia*-group with inverted ovules.

The uncommonly frequent stomata suggest less woody cones than in other taxodiaceans. *Athrotaxis cupressoides* and *Sphenolepis*, with externally similar cones, lack fibrous hypodermal tissue [5]. The inflorescence-like aggregates of seed cones typical for *Globiostrobus* are unique in conifers.

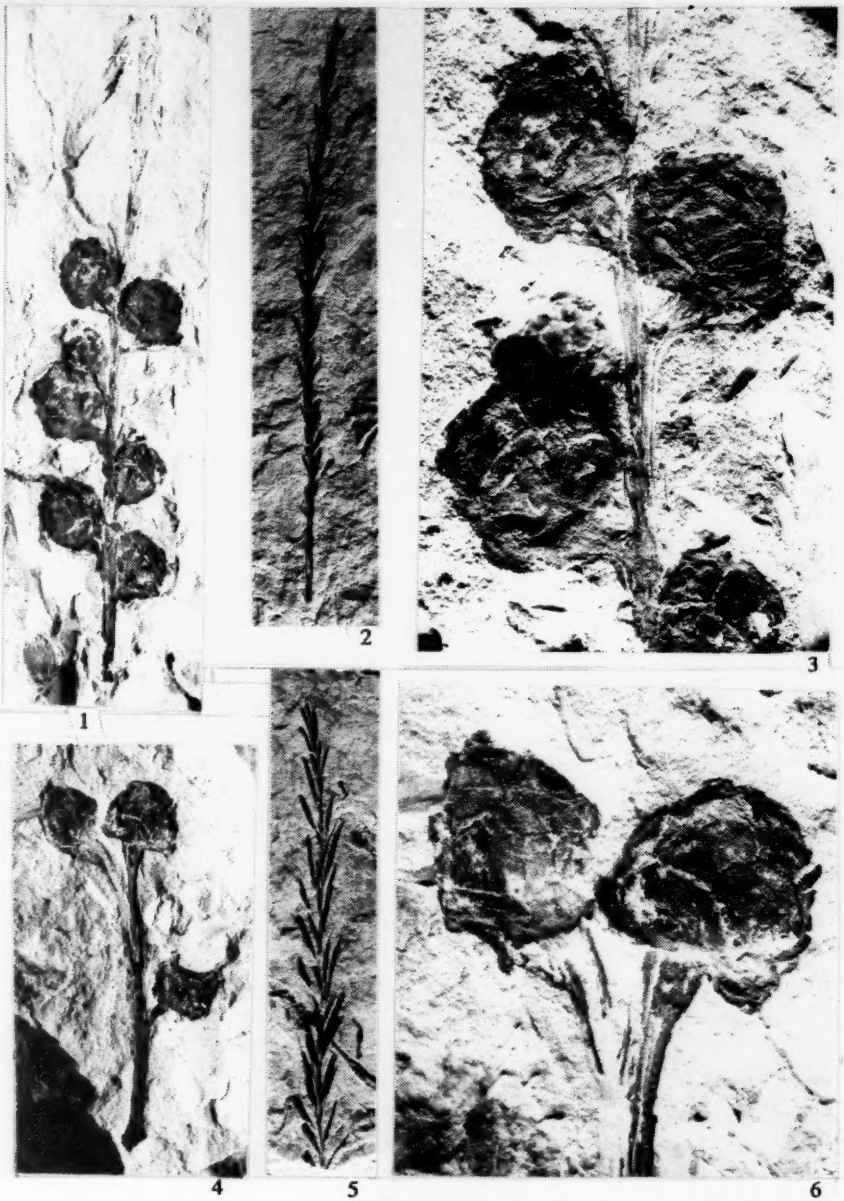

PLATE I

KEY TO PLATE I

Gobiostrobus mongolica Makul.

Figs. 1, 3, 4, 6 - "Inflorescences" of seed cones, 1, 3 - holotype, No. 3985/1-71, Tsagan-Khushu, ×1 and ×3; 4, 6 - No. 3957/10-290, Naran-Bulak, ×1 and ×3; 2, 5 - leafy shoots: 2 - No. 3957/10-354; 5 - No. 3957/10-363, Naran-Bulak.

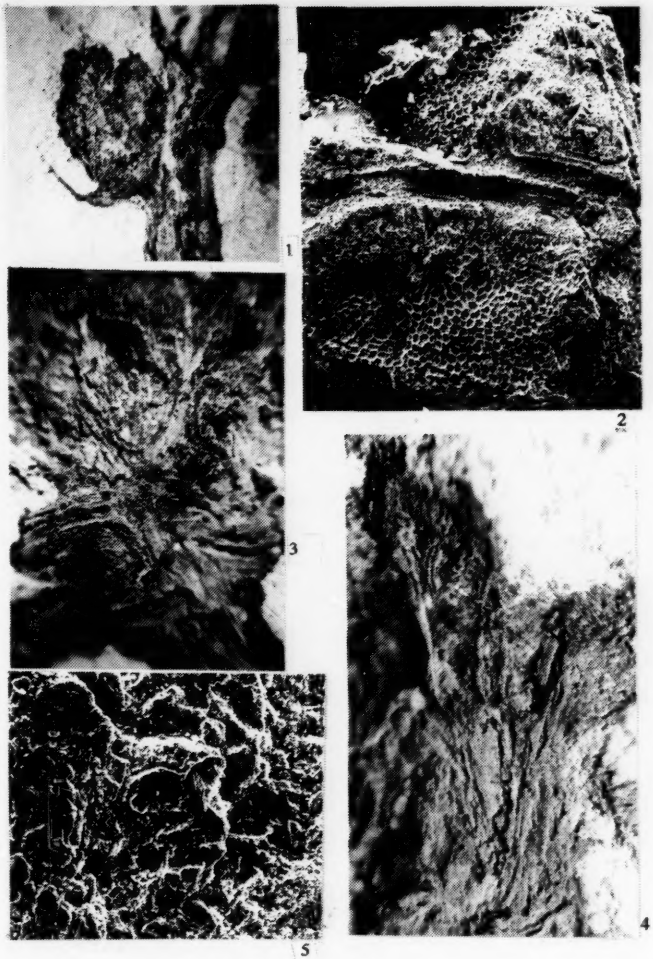

PLATE II

KEY TO PLATE II

Gobiostrobus mongolica Makul.

Fig. 1 - Seed cone scale with seeds, ×5;
Fig. 2 - Cone scale cuticle and stalk showing hypodermal fibers, SEM, ×87;
Fig. 3 - Split cone showing stalks of cone scales and hypodermal fibers;
Fig. 4 - Branching of vascular bundle in cone scale, ×20;
Fig. 5 - Transversely oriented leaf stomata, SEM, ×270.

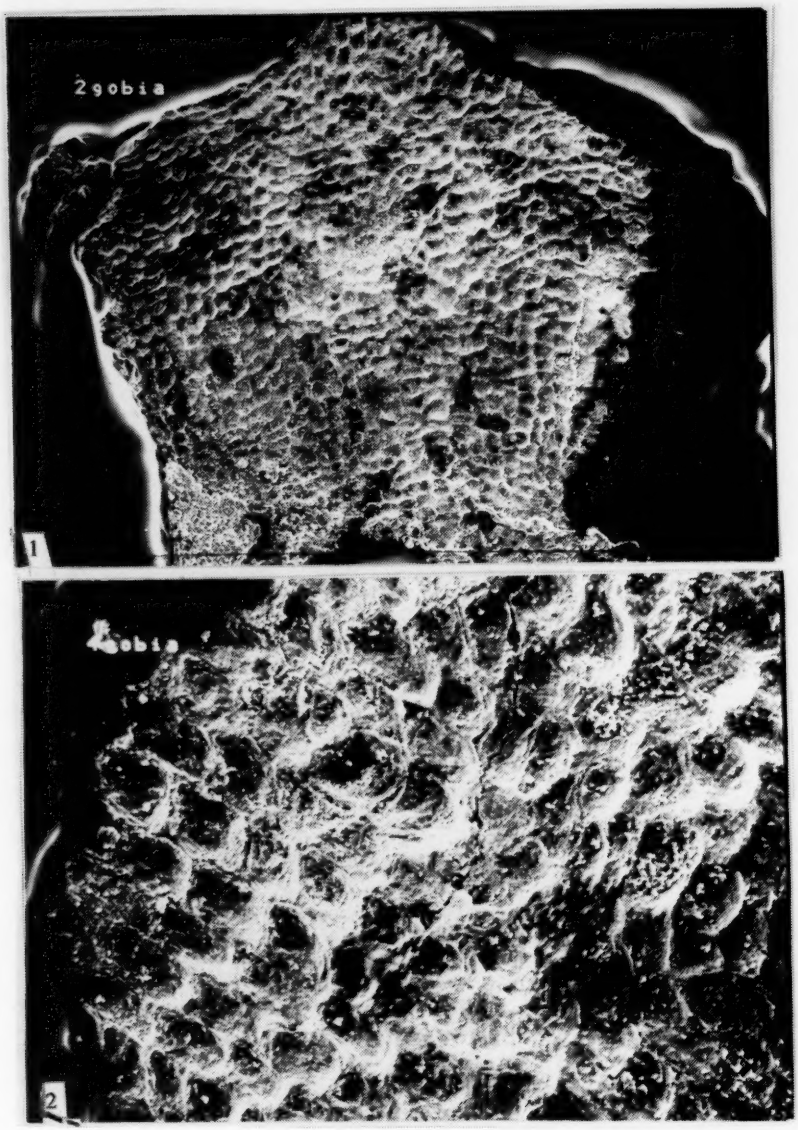

PLATE III

KEY TO PLATE III

Gobiostrobus mongolica Makul.

Fig. 1. - Cone scale shield cuticle replica showing scattered stomata, SEM, ×87;
Fig. 2 - Stomata of above, SEM, ×330.

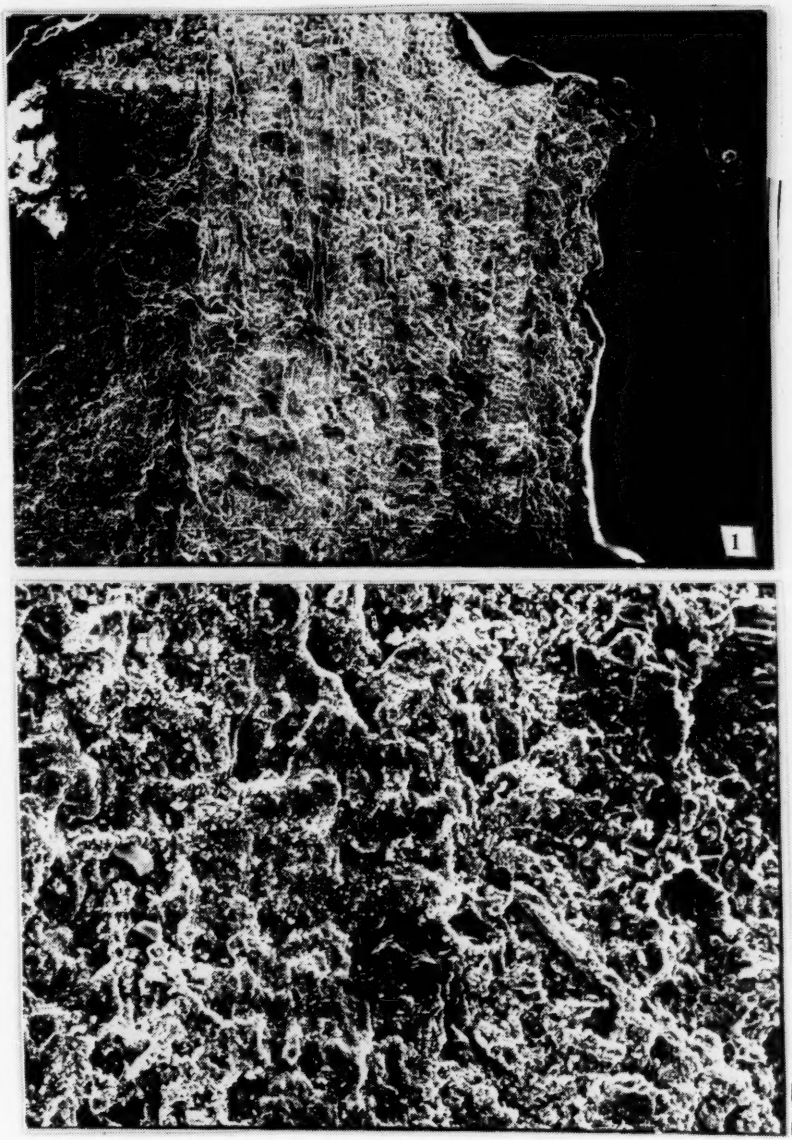

PLATE IV

KEY TO PLATE IV

Gobiostrobus mongolica Makul.

Fig. 1 - Leaf cuticle replica showing stomatal bands, SEM, ×60;
Fig. 2 - Stomata of above, SEM ×370.

Retroconvergence or Gamoheterotopy?

The conventional conifer seed cones are double-strobilate, i.e., they consist of coaxial megastrobili borne in axils of bracts. These structures are more evident in cordaites and Paleozoic conifers than in modern conifers, where the primary megastrobili (seed-scales) or their subtending bracts or both are much reduced or lose their morphological identity in fusion, as the majority of Taxodiaceae.

Incidentally, in *Gobiostrobus* the bract-seed scale complexes are completely fused in the peltate cone scale, and the compact seed cones consist of a small number of such scales. In this conifer, however, the seed cones are typically gathered in "inflorescences," in which they arise in the axils of each successive scale leaf. The "inflorescences" appear as a third round of strobilation involving the much reduced double strobili. Actually, they look much like the progenitorial fertile shoots giving rise to the conventional conifer seed cone.

Two morphological phenomena seem pertinent to the unusual organization of fertile shoots in *Gobiostrobus*. One is retroconvergence, defined by Krassilov in this volume [2], as the tendency of compound organs to convergently resemble their constituent structures (in our case, the seed cones that consist of simple megastrobili in the axils of bracts).

Another phenomenon is gamoheterotopy [4] — the transfer of characters from one sex to another in dimorphic organisms. In a number of conifers, notably the Taxodiaceae, Pinaceae and Podocarpaceae, the pollen cones are gathered in the catkin-like "inflorescences" [1]. It is suggested that this male character was occasionally transferred to the opposite sex, resulting in the seed cone "inflorescences." Perhaps these two possibilities are not mutually exclusive.

Acknowledgment. I thank Professor V. A. Krassilov for his help in the SEM studies and interpretation.

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PETRIFIED WOOD OF *Metasequoia* FROM THE MIOCENE OF KAMCHATKA (KORFA BAY)

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Abstract. *Metasequoia korfiensis* sp. nov., identified by the anatomical features of the fossil wood is described. This fossil wood, from the lower strata of the Medvezhkinsky Suite of late Middle Miocene age, is compared with the wood of living *Metasequoia glyptostroboides* Hu et Cheng and with other woods of fossil *Metasequoia*.

Новый вид *Metasequoia korfiensis* описан по анатомическим признакам древесины. Проведено сравнение с древесиной современного вида и ископаемых метасеквией. Новый вид происходит из нижней части медвежкинской свиты среднего миоцена.

• • •

Metasequoia glyptostroboides Hu et Cheng is the only extant species of the genus *Metasequoia* Miki that occurs as a relict in a small area in Central China; *Metasequoia* was abundant and widespread during the Late Cretaceous and Tertiary in the northern hemisphere.

In spite of the abundance of compression fossils, petrified *Metasequoia* are rare. Five species based on the fossil woods are known (table 1): *Taxodioxylon metasequoianum* Schonfeld from the Upper Oligocene of the Duren brown coalfield in Germany [14]; *Metasequoioxylon hungaricum* Greguss from the Lower-Middle Miocene of Hungary [13]; *Metasequoia sibirica* Shilkina from the Upper Oligocene of western Siberia [10]; *Metasequoia klerkiana* Blokhina from the Eocene-Oligocene of Primor'ye [3, 4]; and *Metasequoia milleri* Rothwell et Basinger from the Middle Eocene of British Columbia, Canada [1].

Description of *Metasequoia korfiensis* sp. nov., identified by the anatomy of the wood, is given here. The petrified wood (19 specimens) was collected by the author from the lower Medvezhkinsky Suite. The stratotype of this suite (500 m thick) is exposed on the western coast of Korfa Bay (Kamchatka) between Okno Cape and the mouth of the Ugolnaya River [6, 7]. The suite lies unconformably on the marine sediments and andesites of the Uspensky Suite and is overlain by the Klassichesky Suite. The boundary between the Medvezhkinsky and Klassichesky suites is at the base of conglomerates at the base of Klassichesky suite. A. I. Chelebaeva [7, 8]

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Table 1. Comparative Anatomy of Wood of Living *Metasequoia glyptostroboides* Hu et Cheng and the Fossils Assigned to *Metasequoia*

Anatomical Characters	Species						
	Metasequoia korfiense Blokhina sp. nov.	*Metasequoia klerkiana* Blokhina [3, 4]	*Metasequoia sibirica* Shilkina [10]	*Metasequoia milleri* Rothwell et Basinger [1]	*Metasequoioxylon hungaricum* Greguss [13]	*Taxodioxylon metasequoianum* Schönfeld [14]	*Metasequoia glyptostroboides* Hu et Cheng [5, 11, 12]
Tracheids: radial pitting-							
uniseriate	+	+	+	+	+	+	+
biseriate	+ +	+ +	+ +	+	+	+	+ +
triseriate	+ -	+ -	+ -	+	-	-	+ -
quadriseriate	-	-	-	+	-	-	-
tangential pitting	+	-	+	+	-	+	+
Crassulae	+	+	-	+	+	+	+
Trabeculae	+	-	+	-	-	-	+
Wood parenchyma- horizontal walls:							
smooth	+	+	+	+	+	+	+
number of nodules	-	-	-	+ -	+ -	1-3	1-5
Rays:							
height (in cells)	1-25(37)	1-20(37)	1-15	1-35(80)	1-20(32)	1-8(17)	1-23(35)
number of biseriate cells	1-6	1-3	-	1	-	-	1-3(8)
ray tracheids	+	?	-	-	+	?	+
Cross-fields - number of pits	1-4(5)	1-4(5)	1-4(5)	1-5	1-3(6)	1-3	1-4
Traumatic resin cysts	+	-	-	+	?	+	+

Remarks: (+) - present, (-) - absent, (++) - prevail, (+-) - sometimes, (?) - unknown

recognized two subsuites on the basis of the lithology and floristic complex. The lower Medvezhkinsky subsuite (100-150 m thick) corresponds to coarse-pebble conglomerates in the base of the sequence. Near the mouth of the Bolshaya Kamenushka River, this subsuite contains a lenticular bed (about 40 m thick) of blue-gray and whitish tuffites, the so-called "blue sandstone." The fossils were collected from this bed. The age of the lower Medvezhkinsky subsuite is late Middle Miocene [7].

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The wood of *Metasequoia korfiensis* sp. nov. was found in four sites. Two sites are on the watershed of the Bolshaya Kamenushka River and its right tributary, Malaya Kamenushka (3 specimens - Nos. 14/715-3, 14/715-5, 14/715-6a), and two other are on the right bank of Malaya Kamenushka (14 specimens - Nos. 14/711-8, 14/711-9, 14/711-13, 14/711-20, 14/711-29, 14/711-33, 14/711-37, 14/711-42, 14/711-51, 14/711-72, 14/711-80, 14/714-12, 14/714-13, 14/714-37). Two more specimens were found in the screes on the right (No. 14/712-1) and left (No. 14/713-5) banks of Bolshaya Kamenushka.

Plant imprints are well preserved in the "blue sandstones" on the right bank of Bolshaya Kamenushka, where *Glyptostrobus europaeus, Populus korfiense*, and *Betula polymorpha* predominate [7].

The leaf imprints of *Metasequoia disticha* (Heer) Miki were found in the lower Medvezhkinsky subsuite near Okno Cape. However, Chelebaeva [7] considers the assignment to this species as provisional, because epidermal analysis has not been made. The *Metasequoia* was found with *Pterocarya kamtschatika, Betula polymorpha, Alnus pojarkovae, Magnolia*(?) sp., *Salix itelmenesis*, and *Acer* sp. *Pterocarya* and *Betula* are prevalent, but not numerous. A. F. Fradkina [9] mentioned common but not numerous *Metasequoia* pollen in the base of the lower Medvezhkinsky subsuite.

Chelebaeva [7] recognized a few riparian assemblages. Slopes of the broad valley were overgrown by mixed forest with *Metasequoia, Thuja, Fagus,* and *Quercus* at the lower belts, and with *Pinus* and *Laris* as dominants upslope. However, the remains of slope vegetation are rare among our imprints. Probably, the valley slopes were far from the site of deposition.

The living *Metasequoia* grows along river valleys, streams and deep canyons at 700-1350 m above sea level. It occurs in groups and in sparse growth or in deciduous mixed forest with an admixture of a few conifers.

The living *Sequoia, Sequoiadendron* and *Metasequoia*, as well as their fossil representa-tives, are difficult to distinguish from each other by wood anatomy. They may be classified into the *Sequoia*-lineage that, unlike the *Taxodium-Glyptostrobus* one, is characterized by the presence of ray tracheids, smooth (or with small nodules) horizontal walls of wood parenchyma, and traumatic resin cysts.

The Cretaceous woods of these Taxodiaceae show a mixture of anatomical features of *Sequoia, Taxodium* and *Glyptostrobus*, i.e., representatives of both lineages. Perhaps they

Table 2. Comparative Dimensions (in μm) of the Wood Structure Elements of Living *Sequoia*-Lineage and Fossils Assigned to *Metasequoia*

Anatomical characters	Species					
	Metasequoia kor-fiense Blokhina sp. nov.	*Metasequoia sibir-ica* Shilkina [10]	*Metasequoia milleri* Rothwell et Basinger [1]	*Metasequoia glyp-tostroboides* Hu et Cheng [1, 5, 11, 12]	*Sequoia sempervirens* Endl. [5, 11, 12]	*Sequoiadendron giganteum* (Lindl.) Buchn. [11, 12]
Diameter of tracheids:						
early wood -						
radial	40-60	42-48	25-95	?	?	?
tangential	30-60	18-30	25-65	?	max 70-80	?
late wood -						
radial	30	17-27	?	?	?	?
tangential	18	18-30	?	?	?	?
Thickness of walls:						
early tracheids	1, 5-3	?	1, 5-2, 5	2-3	2-3	?
late tracheids	3-5	?	4-5	4-6	5-7	?
Radial pitting:						
diameter of pits	17-20	9-11(17)	17-23	18-22	14-17	14-17
diameter of aperture	5-8	?	5-7, 5	?	?	?
Tangential pitting:						
diameter of pits	10-13	?	15-20	9-11 (13-17)	12-14(16)	11-13
diameter of aperture	5	?	5-7	?	?	?
Cross-fields -						
diameter of pits	10-12	?	9-14	10-13	5-6(12)	4, 5-8
Ray cells:						
height	24	?	16-19	15-20(25)	13-30(70)	18-22(26)
width	18	?	13-16	8-16(18)	9-25(40)	?
Wood parenchyma -						
length of cells	132-228	?	70-160	?	?	?

Remarks: (?) - unknown

belonged to an ancestral complex of redwood-like plants, which gave rise, probably, to two main lineages by the Early Tertiary, *Sequoia* and *Taxodium-Glyptostrobus*. The Tertiary woods of these Taxodiaceae show a mixture of anatomical features of *Sequoia*, *Sequoiadendron*, and *Metasequoia* on the one hand and *Taxodium-Glyptostrobus* on the other hand.

The wood anatomy of *Metasequoia* is very similar to *Sequoia* and *Taxodium* as well as Cupressaceae. The presence of abundant biseriate pitting with crassulae on the radial walls of tracheids, wood parenchyma with smooth or slightly thickened horizontal walls, smooth horizontal and tangential walls of the rays are characteristics of both *Metasequoia* and Cupressaceae. Taxodioid pits on the cross-fields are derived from cupressoid ones by reduction of their border. Thus, *Metasequoia* may be a possible connecting link between Taxodiaceae (the group of *Sequoia-Taxodium*) and Cupressaceae. E. S. Chavchavadze [5] believes that the wood structures of both Taxodiaceae and Cupressaceae are at the same stage of evolutionary development. Their evolution resulted in more distinctive characters.

The Late Cretaceous-Tertiary woods of redwood-like plants were described as *Sequoioxylon*, *Taxodioxylon*, *Metasequoioxylon*, and sometimes *Cupressinoxylon*. R. E. Torrey [15] proposed the form genus *Sequoioxylon* for the woods with traumatic resin cysts in addition to the features of Cupressaceae and Taxodiaceae. However, R. Kräusel restricted the name *Sequoioxylon* only for the obvious redwoods, but assigned the others corresponding to the genus *Sequoioxylon* Torrey to the form genus *Taxodioxylon* Goeppert [1].

P. Greguss [13] proposed the form genus *Metasequoioxylon* for the woods with characters on the living *Metasequoia*. Nevertheless, the diagnosis of this form genus included characters of all *Sequoia*-like plants. E. Schönfeld [14] preferred even to restore the name *Taxodioxylon* for the woods with the characters for *Metasequoia*. Thus, it is best to use the name *Metasequoia* Miki for the obvious fossil woods of *Metasequoia*.

Genus ***Metasequoia*** Miki, 1941

Metasequoia korfiensis Blokhina sp. nov.

Pl. I, figs. 1-21

Species name. From the Korfa Bay.

Holotype. Institute of Biology & Pedology, Far East Branch, Russian Academy of Sciences, Vladivostok, No. 14/711-9; Kamchatka, Korfa Bay, Malaya Kamenushka River; lower Medvezhkinsky subsuite, upper Middle Miocene.

Description (pl. I). Growth rings are distinct. Wood is heavily compressed in cross section, judging by the transition from early to late wood and by the width of both zones, as well as by the configurations of tracheids and their dimensions. In the radial section, diameters of early-wood and late-wood tracheids are 40-60 μm and 30 μm, respectively. Diameters of tracheids in tangential section are 30-60 μm and 18 μm, respectively. Thickness of walls of early- and late-wood tracheids are 1.5-3 μm and 3-5 μm, respectively. Ends of tracheids have an obtuse, rounded, sharp and stocking form (pl. I, figs. 4, 5).

PLATE I

Pits on radial walls of early-wood tracheids are abundant. Uniseriate pits are circular, 17-20 μm in diameter, and with circular aperture 5-8 μm in diameter; they are loosely or densely arranged along the walls (pl. I, fig. 1). The biseriate pits predominate; they are oppositely arranged, circular in outline, and with circular aperture (pl. I, fig. 2). There are sometimes three pits in opposite arrangement (pl. I, fig. 3), but they are not well preserved in holotype.

Pits on radial walls of late-wood tracheids are uniseriate, mostly closely arranged along the walls, circular, and with circular aperture, but not well preserved.

Pits on tangential walls of tracheids are separately arranged along the walls, circular in outlines, 10-13 μm in diameter, and with circular aperture 5 μm in diameter (pl. I, fig. 8).

Crassulae are present between biseriate pits, but not well preserved. Trabeculae are rather numerous (pl. I, figs. 10, 11). Traumatic resin canal has been found on radial section. Wood parenchyma is abundant, with resin contents and smooth horizontal walls (pl. I, fig. 9); lengths of parenchyma cells are 132-228 μm.

Rays are numerous, 1-25(37) cells in height, uniseriate, but sometimes with 1-4(6) layers of biseriate cells (pl. I, fig. 6). Two biseriate parts may be found in the same ray. Ray with one layer of triseriate cells is found occasionally (pl. I, fig. 7). Individual ray cells are vertically elongated in tangential section (rounded-rectangular or oval), 24 μm in height, and 18 μm in width; horizontal and tangential walls are smooth. Ray tracheids are present; they are marginal, with thin smooth inner walls (pl. I, fig. 12).

Usually 2-3 taxodioid pits are arranged in one horizontal row on the cross-field in the early wood; rarely, 2 pits are arranged diagonally, or (3)4(5) pits in two rows or irregularly (pl. I, figs. 13-16).

Two pits are usually arranged in horizontal row or diagonally; rarely in vertical row on the cross-field nearer to the late-wood zone, or 3 pits, irregularly or sometimes in one vertical row, and 4 pits in two rows (pl. I, figs. 17-20).

KEY TO PLATE I

Figs. 1-21. *Metasequoia korfiense* Blokhina sp. nov.: 1 - No. 14/711-9, radial section, uniseriate pits on walls of tracheids (×300); 2 - No. 14/711-9, radial section, biseriate pits on walls of tracheids (×300); 3 - No. 14/714-12, radial section, pits on walls of tracheids (×300); 4 - No. 14/711-9, radial section, sharp ends of tracheids (×500); 5 - No. 14/711-9, radial section, rounded ends of tracheids (×300); 6 - No. 14/711-9, tangential section, 6 layers of biseriate cells in ray (×200); 7 - No. 14/711-9, tangential section, triseriate ray (×200); 8 - No. 14/711-9, tangential section, pits on walls of tracheids (×300); 9 - No. 14/711-9, radial section, trabecula (×300); 11 - No. 14/711-9, radial section, trabecula (×500); 12 - No. 14/711-9, radial section, ray tracheid (×300); 13, 16, 17, 19 - No. 14/711-9, radial section, cross-field pitting (×500); 14 - No. 14/711-9, radial section, cross-field (×500); 15 - the same (×800); 18, 20 - No. 14/711-9, radial section, cross-field pitting (×300); 21 - No. 14/711-9, radial section, cross-field pitting (×200); Kamchatka, Korfa/Bay, lower Medvezhkinskian subsuite, late Middle Miocene.

There are 1-2 pits arranged in a vertical row or diagonally, sometimes in horizontal row on the cross-field in the late wood (pl. I, fig. 21).

Diameters of the pits on the cross-field are 10-12 μm.

Comparison. Such anatomical features as the presence of taxodioid pits on the cross-fields and abundant wood parenchyma indicate that this fossil wood belongs to the family Taxodiaceae. Among Taxodiaceae, the *Sequoia*-lineage includes such genera as *Sequoia, Sequoiadendron* and *Metasequoia*, and is characterized by the presence of ray tracheids, traumatic resin cysts, and smooth horizontal walls of wood parenchyma.

These genera are difficult to distinguish from each other by wood anatomy, although some differences may be evident. While resin cysts may be found in all wood of *Sequoia* and *Metasequoia*, they are restricted to the juvenile wood and seed cone axes of *Sequoiadendron*. There are some differences in the diameters of pits in the radial walls of tracheids. *Metasequoia* differs from others in having the largest diameter of bordered pits on the radial walls of tracheids and on the cross-fields as well (table 2). Thus, this fossil wood is similar to the wood of living *Metasequoia*.

Such anatomical features as the type of cross-field pitting, pitting on the radial walls of tracheids, height and structure of the rays, number of pits on the cross-field, and the presence of trabeculae also testify to the resemblance of our fossil wood with the wood of living *Metasequoia*. However, *Metasequoia glyptostroboides* slightly differs from the fossil in having rays not more than 35 cells in height and not more than 4 pits on the cross-field, as well as the occasional presence of 1-5 small nodules on the horizontal walls of wood parenchyma and up to 8 layers of biseriate cells in the uniseriate rays (table 1). Also, a ray with one layer of triseriate cells has been found in the fossil wood.

The described fossil wood closely resembles *Metasequoia klerkiana* Blokh. (table 1) from the Eocene-Oligocene of Primor'ye [3, 4]. However, such anatomical features as the presence of ray tracheids, trabeculae, and pits on the tangential walls of tracheids are not mentioned in the description of *M. klerkiana* (perhaps not preserved), nor are the dimensions of the wood structure elements. There are no resin contents in wood parenchyma and no more than 3 layers of biseriate cells in the rays of *M. klerkiana*. Besides, the described fossil wood differs from *M. klerkiana* in sometimes having two biseriate parts in the same ray, and the presence of a triseriate ray. Thus, this fossil wood should be identified as a new species, *Metasequoia korfiensis* sp. nov.

Remarks. Wood anatomy of the fossil *Metasequoia* from Kamchatka is very similar to the fossil species from Primor'ye (table 1). If the well-preserved specimens from Primor'ye had the same dimensions of woody structures, these two fossil woods might be assigned to the same species. Both *Metasequoia klerkiana* and *M. korfiensis* are closely similar to the living *M. glyptostroboides*.

However, the identification of the fossil wood from Siberia as *Metasequoia* seems rather doubtful. Diameter of pits on the radial walls of tracheids in *M. sibirica* is 9-11(17) μm, while in the living *Metasequoia* it is 18-20 μm (P. Greguss [11, 12] - 20-22 μm), in *Sequoia* - 15-17 μm (P. Greguss [11, 12] - 14-16 μm) and in *Sequoiadendron* - 14-17 μm (table 2). Diameter of the pits in *Taxodium* is 10-15 μm [5, 11, 12]. The fossil wood of *M. sibirica*, like that of *Taxodium*,

is characterized by the absence of ray tracheids and resin cysts. It follows that the fossil wood from Siberia is closer to the genus *Taxodium*.

In addition, leaf-bearing shoots of *Taxodium dubium* are abundant in the Shestakov Log locality, from which the wood of *Metasequoia sibirica* has been described. Cone scales and seeds of *Taxodium dubium* were abundant in the adjacent outcrops as well. Cones of *Sequoia langsdorfii* were found 850 m from Shestakov Log, while the cones of *Metasequoia distincha* (although abundant) were collected 80 km from Shestakov Log [10].

The attribution of the fossil wood from Hungary to *Metasequoia* is also somewhat doubtful (table 1), judging from the description that fossil wood includes characters of the whole *Sequoia*-lineage. Also, P. Greguss [13] did not mention dimensions of the wood structure elements, and the diameter of pits on the radial walls of tracheids is a major diagnostic feature of *Metasequoia*.

Metasequoia milleri from the Middle Eocene of Canada (table 1) is distinguished by the presence of quadriseriate pits on the radial walls of tracheids and has the highest rays (up to 80 cells in height). If these were not with the petrified wood and other parts obviously belonging to *Metasequoia*, that fossil wood might be identified as *Sequoia*.

Variability of leaf anatomy is greater in *Metasequoia milleri* than in *M. glyptostroboides*, and is quite identical to the latter; it resembles *Sequoia, Taxodium* and *Glyptostrobus* as well as *Metasequoia*. According to J. F. Basinger [1] the leaves of *M. milleri* are of a more generalized structure and probably represent the type of leaf from which living species of these Taxodiaceae have been derived. The organic connections of pollen cones, twigs and leaves of *M. milleri* are known. However, other organs have been linked by Basinger [1, 2] on the basis of consistent association, morphological similarity, presence of only a single type of each organ, and independent identification of various organs as *Metasequoia*. The great resemblance of *M. milleri* and *M. glyptostroboides* to each other in the most of their organs except leaf and wood (in some characters) structure may perhaps testify to mosaic evolution within the genus [1, 2].

Metasequoia korfiense is also characterized by the presence of a feature typical for *Sequoia* — a triseriate ray. However, that ray is the only one that has been found in the wood and includes only one layer of triseriate cells. Pollen and leaf impressions of *Metasequoia*, in addition to petrified wood, were found in the Korfa locality. Thus, they are also arguments for the presence of *Metasequoia* there.

In conclusion, it should be noted that hybridization is characteristic of the living Taxodiaceae, including the *Sequoia*-lineage. Probably, it also occurred in the past. Therefore, the different combinations of characters of the *Sequoia*-lineage genera might have appeared as a result.

Locality. The lower Medvezhkinsky subsuite, Medvezhkinsky Suite, Korfovsky Series, upper Middle Miocene, Korfa Bay, Kamchatka.

Material. Nos. 14/711-8, 14/711-9 (holotype), 14/711-13, 14/711-20, 14/711-29, 14/711-33, 14/711-37, 14/711-42, 14/711-51, 14/711-72, 14/711-80, 14/712-1, 14/713-5, 14/714-12, 14/714-13, 14/714-37, 14/715-3, 14/715-5, 14/715-6a. Nineteen solid fragments of lignified secondary wood are dark brown to black in color, heavily compressed in cross-section, and 5 × 7 × 10 cm in mean size.

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CENOZOIC HISTORY OF *Nyssa* L. (NYSSACEAE) IN NORTHERN ASIA

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Abstract. Cenozoic records of *Nyssa* L. from northern Asia are reviewed. A few fossil leaves, previously identified as *Magnolia* and *Quercus*, are now recognized as belonging to *Nyssa*. Several new nomenclatorial combinations are proposed and a new Paleocene Far Eastern species is described. The Cenozoic north Asian history of the genus discussed.

Дан обзор находок *Nyssa* L. в кайнозое северной Азии. Некоторые ископаемые листья, ранее относимые к *Magnolia* и *Quercus*, переопределены как *Nyssa*. Установлен новый вид и предложены новые номенклатурные комбинации. Рассмотрена кайнозойская история рода.

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Introduction

The extant *Nyssa* L. is a relict genus with disjunct ranges [8]. Its area of distribution — southeastern North America, part of Central America, Central China, and southeastern Asia — and separated by the Pacific, testifies to the wide geographical distribution and the long-term history in the Cenozoic.

Two genera — *Nyssa* L. and *Camptotheca* Decne — form the family Nyssaceae Juss. *Nyssa* includes six extant species from tropical and subtropical latitudes on both sides of the Pacific as well as on the Atlantic coast of southeastern North America [8, 9, 28] (fig. 1).

The extant species of *Nyssa* fall into two rather distinct groups on the basis of leaf characters: serrate-margined (*N. aquatica* L.) and entire-margined (*N. biflora* Walter, *N. javanica* (Bl.) Wangerin, *N. ogeche* Marshall, *N. sinensis* Oliv.). *N. sylvatica* Marshall has mainly entire-margined leaves, but some of them have irregular dentate leaves with large deltoid teeth [8, 9]. *N. sylvatica*, *N. biflora* and *N. sinensis* not only have similar morphological characters but also live in similar habitats, and are grouped into the "*Nyssa sylvatica* complex" [8] (fig. 1). *N. sinensis* is considered the most primitive in the genus [27].

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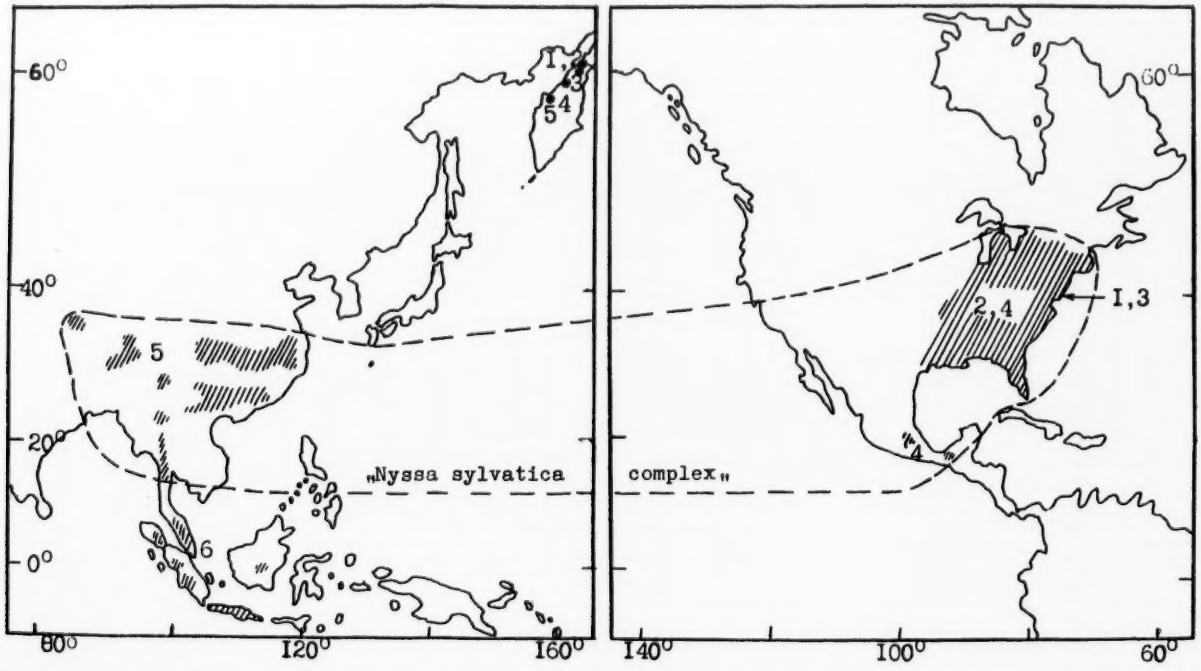


Fig. 1. The modern distribution of genus *Nyssa* (according to [8, 28]) and fossil records of *N. budantsevii* sp. nov.

Ranges of extant species: 1 - *N. aquatica* L.; 2 - *N. biflora* Walter; 3 - *N. ogeche* Marshall; 4 - *N. sylvatica* Marshall; 5 - *N. sinensis* Oliver; 6 - *N. javanica* (Bl.) Wangerin.

Ranges of "*N. sylvatica* complex" [8].

• Fossil records of *N.budantsevii* sp. nov. in western Kamchatka: 1 - Chemurnaut Bay; 2 - Evrava-veyem River; 3 - Rebro-Getkilnin Bay; 4 - Anadyrka River; 5 - Snatol River.

Nyssa was widespread during the Cenozoic in Europe, northern Asia and North America, as is shown by the leaf impressions, fruits, wood, and pollen grains. The leaf epidermal structure of *N. haidingerii* (Ett.) Kvacek et Buzek from Europe has been studied [22].

Fossil records of the genus in eastern Asia extend from the very beginning of the Cenozoic [18] to the Late Miocene [2]. There were no records older than the Eocene in the European part of Russia, Kazakhstan and Siberia. Thus, the earliest appearance of *Nyssa* is connected with the western Pacific margin.

The Identification Problem

Nyssa leaves with large teeth resemble *Quercus* and some of the European and Kazakhstanian floras were actually described as *Quercus* [16, 17, 22, 31]. Entire-margined leaves of *Nyssa* greatly resemble a number of genera such as *Magnolia, Laurus, Persea, Coccoloba, Cinchonidium*, and others [22]. In this connection, some authors find it very difficult to define the entire-margined nyssoid morphotype on the basis of the leaf gross morphology alone, and rely on epidermal structures. Vikulin and Pneva [29], however, believe that it is possible to define *Nyssa* on the basis of the tertiary and higher order venation, the leaf form, and the divergence of the secondary veins at the leaf base.

Reviews of the literature on northern Asia and Kazakhstan have enabled establishment of new records of *Nyssa* that were originally assigned to other genera.

The nyssoid morphotype was described as the holotype of *Magnolia ochotica* Budants., from the lower part of the Middle Eocene seashore terrigenous section near the mouth of Anadyrka River, western Kamchatka [6; pl. 14, fig. 1](fig. 2). It is characterized by the secondary veins that sometimes fork within one-third of the distance to the margin. The ends of the forking veins join in angular loops. A thin tertiary branch arises from the brochidodromous secondary arch, reaching small marginal dents. Other specimens from this locality may actually belong to *Magnolia*.

Quercus tsagajanica Poyark. was described from the Danian Tsagajan Formation (Bureyinskiy Tsagajan locality) of the Zeya-Bureya Depression from the continental Russian Far East [26] (fig. 3). V. Krassilov [18] regards it as synonymous with *"Platanus" reynoldsii* Newb. This species has rather prominent irregular venation with some secondaries forking at one-fourth to one-half the distance to the margin. The forking ends of secondary veins form long loops. The margin is irregularly dentate; teeth are short with shallow sinuses between them. All these characters are typical for *Nyssa*.

Quercus alexeevii Poyark. was first identified from the northern area of the Aral Sea, Kazakhstan [26]. It was later found in many localities in Kazakhstan and Siberia [15, 16, 29, 31] (fig. 4). The analysis of the Upper Oligocene-Aquitanian *Q. alexeevi* from Kazakhstan enabled us to distinguish two separate groups. The morphological distinctions between these groups are especially evident in the basal and apical regions of the leaves. The first group, including the holotype, has secondary veins running parallel to the leaf base (fig. 5, 1). The second group has converging based secondaries at straight (nearly straight) angles to the midrib. In the distal part of the leaf the first group has the distant, gently upcurving secondaries diverging form the midrib at 40-50°. In this case the marginal loops are not evident. In the second group there are wider

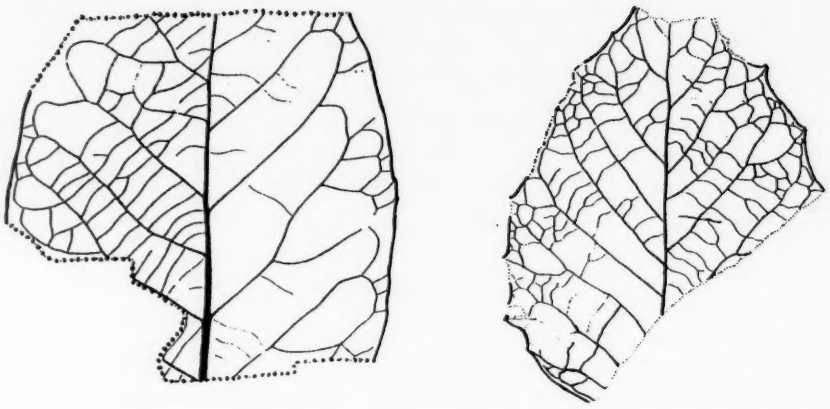


Fig. 2. *Nyssa* sp. ([6], pl. 14, fig. 1, sub. nom. *Magnolia ochotica* Budants., Holotype, western Kamchatka, Anadyrka River, Paleocene-Early Eocene), ×0.73.

Fig. 3. *Nyssa tsagajanica* (Poyark.) Fotyan. ([26], fig. 10, sub. nom. *Querus tsagajanica* Poyark., holotype [lost], Far East, Bureya Tsagajan, Tsagajan Formation, (Danian), ×.73.

angles of diverging (55-60°) and the veins are obviously brochidodromous (fig. 5, 2). The first group has irregulate dentate margin with rare obtuse teeth without bristles. The second group has acute teeth with pointed ends, sometimes with bristles.

We believe that the material described under the name *Quercus alexeevii* from Kazakhstan falls into different genera. The first group, including holotype, is undoubtedly close to *N. aquatica* (figs. 5, 1; 4, 15-18). The second one might belong in the genus *Quercus*, as was suggested by A. I. Poyarkova [25].

The most ancient *Nyssa* (*N. tschucotica* Golovn.) was reported from the Maastrichtian in the Koryak Highlands, northeastern Asia [14]. The leaves of this species are most variable, some showing characters alien to *Nyssa* (ovate-triangular and ovate-triangular-cordate shape; cordate or slightly reniform and decurrent base; secondaries vanishing toward margin; rounded teeth). At the same time, some characters of *N. tschucotica* are similar, though not quite characteristic of *Nyssa* [14; fig. 2, 1, 2]. The combination of these two types of characters allows the suggestion that it was actually a Nyssaceae closely related but not congeneric to *Nyssa*. According to Tanai [28], most Cretaceous nyssoid fossils seem doubtful. According to Markevich [24], the formal genus *Nyssepollenites* has been found in the Maastrichtian of Primor'ye.

The above considerations enable suggestion of the following nomenclatural changes:

Nyssa sp. for *Magnolia ochotica* Budantsev
Nyssa tsagajanica (Poyark.) Fotyan., comb. nov. for *Quercus tsagajanica* Poyark.
Nyssa alexeevii (Poyark.) Fotyan., comb. nov. for *Quercus alexeevii* Poyark. (partly).

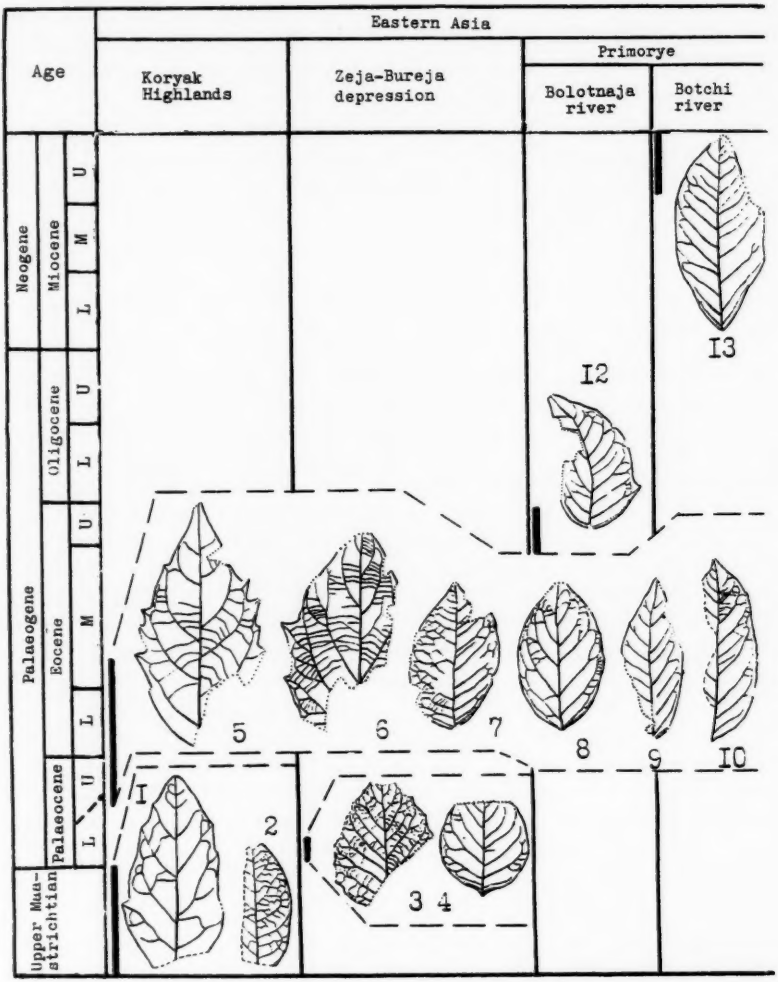
Kamchatkan Material

I have collected extensive material from many Paleocene-Eocene localities in western Kamchatka. The leaf material described in here is in the Paleontological Institute, Russian Academy of Sciences, Moscow: Collections No. 3736 - Chemurnaut Bay and Evrava-veyem River; No. 3858 - Anadyrka River; No. 4256 - Snatol River (Kamchatka). It is mostly entire-margined leaves and a few toothed and sarrate-margined leaves typical of *Nyssa*; these enable construction of a pattern of variation (fig. 4) from the gross-dentate through minutely dentate, and from occasional teeth to entire-margined type. As mentioned, the entire-margined type could hardly be identified by itself. The leaf polymorphism analysis has shown that *Nyssa* was widespread in the terminal Paleocene-Middle Eocene floras of western Kamchatka.

New records of *Nyssa* from Kamchatka and the revision of the previous records from Kazakhstan and East Asia have made it possible to outline the Cenozoic history of *Nyssa* in northern Asia.

Note: On Figure 4, see pp. 118-119.

Fig. 4. Distribution of extinct *Nyssa* species in the Cenozoic of northern Asia: 1, 2 - "*Nyssa*" *tschucotica* Golovn. ([14], sub. nom. *Nyssa tschucotica* Golovn.: 1 - Coll. 1199, No. 158; 2 - Coll. 967, No. 1201. Koryak Highland, Gornaya River, Rarytkin Formation, middle subformation, Maastrichtian); 3 - *N. tsagajanica* (Poyark.) Fotyan. ([26], sub. nom. *Quercus tsagajanica* Poyark., holotype [lost]. Far East, Bureya Tsagajan, Tsagajan Formation, Danian); 4 - *N. bureica* Krassil. ([18], Coll. 575, No. 174, holotype. Far East, Bureya Tsagajan, Tsagajan Formation, Danian). 5-11 - *N. budantsevii* Fotyan., sp. nov., western Kamchatka: 5 - Coll. 4256, No. 2/77-106b, holotype. Snatol River, Napana Formation, Upper Paleocene; 6 - Coll. 3858, No. 20A/75-4, terrigenous beds north of mouth of Anadyrka River, lower part of Middle Eocene; 7, 9, 10 - Coll. 3736: 7 - No. 10A/75-24; 9 - No. 10/75-37; 10 - 10A/75-39, Chemurnaut Bay, upper part of Kamchik Formation, Upper Paleocene; 8, 11 - Coll. 3736: 8 - No. 6/87-21; 11 - No. 6/87-24, Evrava-veyem River, upper part of Kamchik and/or lower part of Tkaprovayam formations, Upper Paleocene. 12 - *N. komarovii* Ablaev et Akhmetiev ([1], pl. 11, fig. 2, No. 638/42. Primor'ye, Bolotnaya River, Bolotninskaya Formation, Upper Eocene (according to [21]). 13 - *N. pseudoaquatica* Akhmetiev ([2], Coll. 3805, No. 1281, holotype. Primor'ye, Botchi River, Botchi Formation, Upper Miocene). 14 - *N. a-yokajamai* Tanai ([28], No. 25972, holotype. Western Honshu, Kobe, Shirakawa Formation, boundary of Lower and Middle Miocene). 15-18, 22 - *N. alexeevii* (Poyark.) Fotyan.: 15-18 - Kazakhstan: 15 - Saribulak, Upper Oligocene-Aquitanian (according to [31]); ([25], sub nom. *Quercus alexeevii* Poyark., holotype, Fig. 7; Coll. 6358, No. 29; [11], pl. 69, fig. 1; fig. 79-1); 16 - Kin-Tykche Gully, northern area of Aral Sea, Aquitanian ([31], sub. nom. *Quercus alexeevii* Poyark.; pl. 26, fig. 2; fig. 13-1; Coll. 1013, No. 6); 17 - Kin-Tykche Gully, northern area of Aral Sea, Aquitanian ([31], sub. nom. *Quercus alexeevii* Poyark., fig. 12; Coll. 1013, No. 10A); 18 - Ashutas, Aquitanian (according to [31]); ([20], sub. nom. *Quercus alexeevii* Poyark., pl. 32, fig. 4; Coll. 2113, No. 441; [11], sub. nom. *Quercus alexeevii* Poyark., pl. 69, fig. 2; fig. 78-2); 22 - western Siberia, Tim River, Miocene ([15], sub. nom. *Quercus alexeevii* Poyark., pl. 72, fig. 2); 19, 20 - *N. zhilinii* Vikulin et Pneva. Eastern Kazakhstan, Ashutas, Aquitanian (according to [31]). 19 - ([29], pl. 1, fig. 4; fig. b; Coll. 2113, No. 78), 20 - ([29], holotype, pl. 1, figs. 1, 2, 3; Coll. 2113, No. 1375), 21 - *N. europaea* Ung. ([15], pl. 73, fig. 3. Western Siberia, Tim River, Miocene). All figures ×0.25-0.30.


Age
Eastern Asia
Primorye
Koryak Highlands
Zeja-Bureja depression
Bolotnaja river
Botchi river
Neogene
Miocene
Palaeogene
Oligocene
Eocene
Palaeocene
Upper Maastrichtian
L
M
U
I
2
3 4
5
6
7
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9
I0
I2
I3

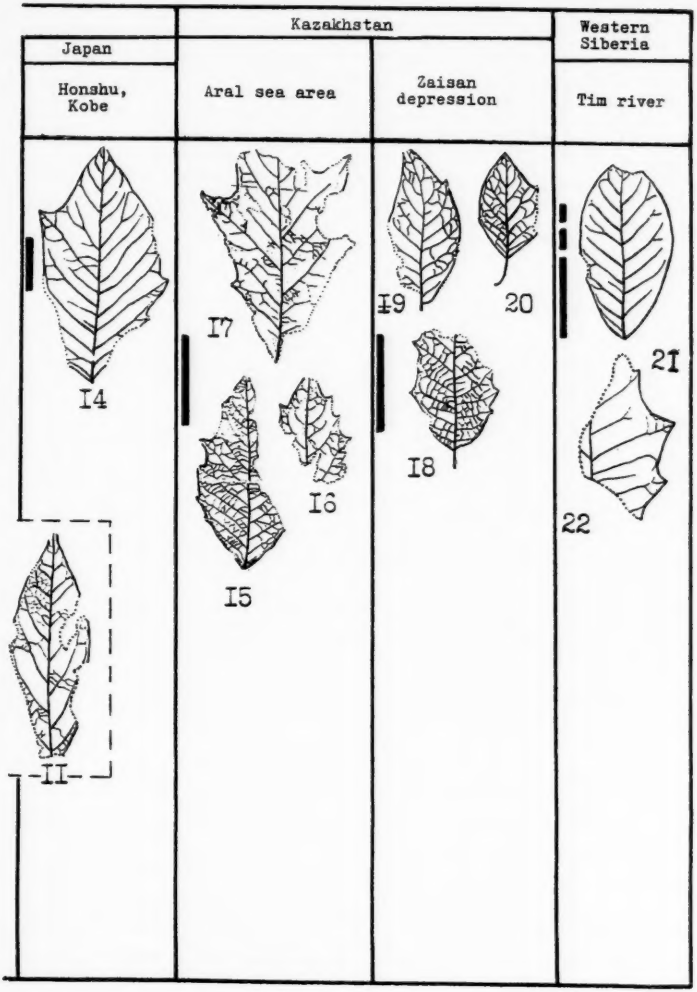
Japan
Honshu, Kobe
Kazakhstan
Aral sea area
Zaisan depression
Western Siberia
Tim river
I4
I7
I6
I5
I9
20
I8
21
22
II

Table 1. Measurements of *Nyssa budantsevii* Fotyan., sp. nov.

Specimens, Nos.	Length, cm	Width, cm	Length to width ratio	Leaf shape
2/77-106b, Holotype	19	10	10:5	Acute-elliptical
20 A/75-4	18	11	10:6	-"-"-
10a/75-24	11	6.5	10:6	-"-"-
2/75-18	12	7	10:6	-"-"-
8/82-3A	16	8	10:6	-"-"-
6/87-21	12	6	10:5	-"-"-
20a/75-13	15	7	10:5	-"-"-
20a/75-107	18	9	10:5	-"-"-
8/75-6	10	5	10:5	-"-"-
10/75-38	18	8	10:4	Broad-lanceolate
6/87-4	16	7	10:4	-"-"-
10A/75-37	14	6	10:4	-"-"-
10A/75-39	12	5	10:4	-"-"-
6/87-24	12	4	10:3	Lanceolate

Historical Sketch

The ancestry of the Early Cenozoic *Nyssa* could probably be related to the Late Maastrichtian "*Nyssa*" *tschucotica* [14]. It is interesting to note that in this Maastrichtian species were both serrate- and entire-margined types (figs. 4-1, 2). It is possible to trace these morphotypes in the Paleogene and Miocene of eastern Asia. They are known from the Danian Tsagajan flora (*N. bureica* Krassil. - *N. tsagajanica* (Poyark.) Fotyan.), from the latest Paleocene -Middle Eocene of western Kamchatka (*N. budantsevii* sp. nov.), from the Miocene of western Siberia (*N. europaea* Ung. - *N. alexeevii* (Poyark.) Fotyan.), from the Paleogene and Miocene of the Far Eastern region of Russia Primor'ye (*N. komarovii* Ablaev et Akhmetiev - *N. pseudoaquatica* Akhmetiev), and from the Miocene of Japan (*N. a-yokajamai* Tanai)(fig. 4).

The continuous development of *Nyssa* is traceable almost through the entire Cenozoic of the Russian Far East. In Siberia and Kazakhstan the genus is known from the Late Paleogene to Middle Miocene. It should be noted that the Upper Oligocene-Aquitanian *N. alexeevii* from Kazakhstan was very similar to the Kamchatkian Upper Paleocene-Middle Eocene *N. budantsevii*. It seems plausible that *N. alexeevii* is phylogenetically related to *N. budantsevii*.

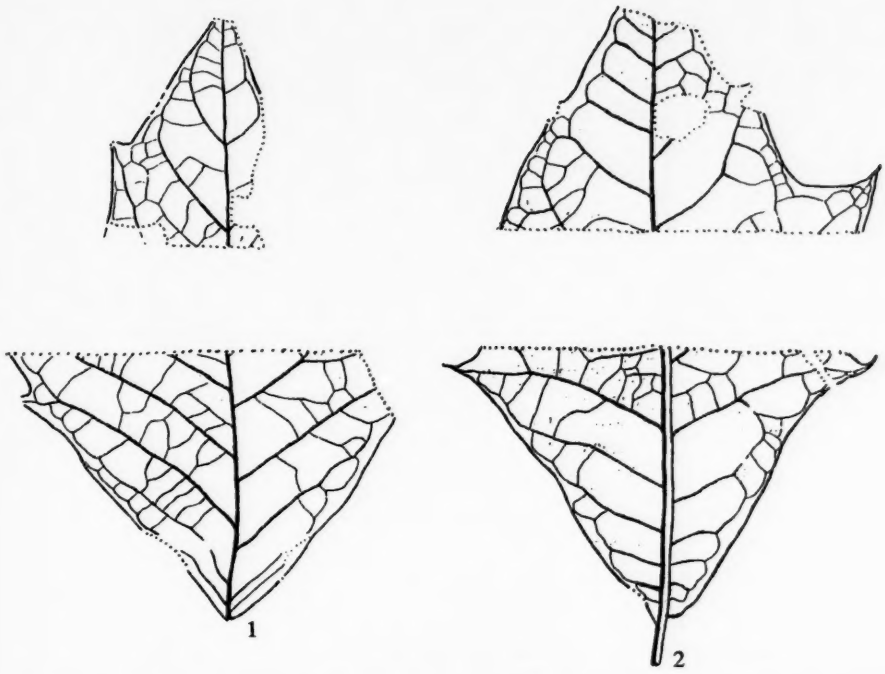

Fig. 5. Morphological distinction between *Nyssa* and *Quercus*, originally described as *Quercus alexeevii* Poyark. from Kazakhstan. 1 - *Nyssa alexeevii* (Poyark.) ([25], sub. nom. *Quercus alexeevii* Poyark., holotype, fig. 7; Coll. 6358, No. 29); [11], sub. nom. *Quercus alexeevii* Poyark., pl. 69, fig. 1; fig. 79-1. Saribulak, Upper Oligocene-Aquitanian (according to [31]); 2 - *Quercus "alexeevii"*, [11], fig. 79-2. Ashtas, Aquitanian (according to [31]).

Nyssa, as the oldest Arcto-Boreal (Greenlandian, according to Kryshtofovich [19]) floristic element, appeared in northeastern Asia, probably in the former Beringia territories. Subsequently, it might have spread to the west across eastern and western Siberia and Kazakhstan, and to Europe after the Turgay Strait was closed in the Early Oligocene.

The peculiarity of the historical development of *Nyssa* in the Cenozoic of northern Asia is that this genus has never been rich in species, and the few recognizable species seem to have succeeded each other in time (fig. 6). There was no adaptive radiation in the Cenozoic, in contrast to many other broad-leaved flowering plants.

The palynological data help to decipher the historical development of *Nyssa*. According to these data, *Nyssa* pollen was not found in the Paleocene of northeastern Asia. Eocene *Nyssa* pollen grains have been reported from northern Middle Yakutia (70°N)[4], New Siberian Islands (76°N)[13], and northern Chukotka [3]. These localities represent the northernmost occurrence of the genus in the Early-Middle Eocene. The most southern Middle-Upper Eocene *Nyssa* are known from Hokkaido [28]. Upper Eocene *N. komarovii* was identified from the Bolotnaya flora in Primor'ye [1, 21].

PLATE I

There was a partial extinction of the genus and sharp reduction of its ranges during the Oligocene. In eastern Asia, *Nyssa* megafossils have been found in the Oligocene of Hokkaido [28]. It should be noted that in Kazakhstan *Nyssa* megafossils first appeared in the Upper Oligocene [29].

Short-term recurrence of *Nyssa*, based on palynological data, was recognized around the Early-Middle Miocene boundary. A few records of the genus were established in northern Chukotka [3], Kamchatka, northern Okhotsk coast, and Sakhalin [12].

Nyssa almost disappeared from the mid and high latitudes in the Far East until the end of the Middle Miocene. It was preserved, however, in Primor'ye until the end of the Miocene [2], and in Hokkaido until the Late Pliocene [30].

Thus, the history of *Nyssa* has been traced from the earliest Paleogene of northeastern Asia, then to the west through Siberia during the Eocene-Oligocene. The discontinuous extinction, with a brief recurrence in the Middle Miocene and the forming of the extant range, is documented in eastern Asia from the Early Oligocene.

Nyssa budantsevii Fotyanova, sp. nov.

Pl. I, figs. 1-3; Pl. II, figs. 1-3, Pl. 3, figs. 1-7

Holotype. Coll. 4256, No. 2/77-106b. PIN RAN, impression of nearly complete leaf. Western Kamchatka, Snatol River; 1.85 km east of mouth of Tatyana Spring, isolated block of Napana Formation, Upper Paleocene.

Material. Coll. 4256, No. 2/77-106b; Coll. 3858, Nos. 15A/77-9, 19/75-12, 20A/75-4, 5, 13, 23, 103, 107; Coll. 3736, Nos. 10/75-38, 10A/75-14, 27, 37, 39; 6/87-4, 21, 24; 2/75-18; 8/75-6, 8/82-3a; and others.

Description. Leaves are rather large, mostly 12-15 cm long (sometimes over 19 cm), 4-11 cm wide, typically widest in middle part, acute-elliptical (ratio of length to width 10:5-10:6), broad-lanceolate (10:4), and lanceolate (10:3).

Base is short to long cuneate, rarely rounded, and symmetrical or slightly asymmetrical. Apex gradually narrows with elongate acuminate point. Brochidodromous venation is rather prominent, with thick midrib especially in the lower 1/3 and with 7-14 alternate or subopposite irregularly spaced secondaries arising at 50-70° in the lower part of the leaf and at 45-60° in the

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KEY TO PLATE I

Figs. 1-3 - *Nyssa budantsevii* sp. nov., western Kamchatka. 1, 2 - Coll. 3736, No. 8/87-11, Evrava-veyem River, upper part of Kamchik and/or lower part of Tkaprovayam formations, Upper Paleocene. 1 - ×2.0; 2 - ×0.8. 3 - Coll. 4256, No. 2/77-106b, holotype, ×0.8, Snatol River, Napana Formation, Upper Paleocene.

PLATE II

middle part, as well as near the apex. Secondaries on one side of the midrib are often at more acute angles than on the opposite side. They typically fork distally, but occasionally in the lower 1/2 or 2/3 of the distance to the margin, abruptly turning up near the margin. They usually give off several distal branches; these outer branches end in teeth (in serrate-margined leaves), or form loops along the margin with the succeeding secondary veins (in entire-margined leaves).

Intersecondaries are infrequent. They appear as short, weak secondaries; tertiary veins are rather regularly percurrent, sometimes slightly oblique and forking. The quaternary veins form large quadrangular or pentagonal meshes.

The leaf margin is quite variable: entire, wavy, with rare minute teeth, or irregularly dentate with large deltoid teeth. Where large teeth occur, a thick tertiary branch of the brochidodromous secondary arch runs to the apex of the teeth. Usually teeth occur in the middle and upper parts of the blade, but occasionally in the basal part also. Textura is thin.

Discussion. The holotype and other gross-dentate specimens are rather similar to *Nyssa a-yokojamai* Tanai from the Middle Miocene Kobe group of western Honshu, Japan [28]. The Kamchatkan species is distinguishable by the distant, brochidodromous, arched secondaries with the branch terminating in the marginal teeth. Serrate-margined *N. a-yokojamai* has camptodromous secondaries.

My species is comparable to the North American *Nyssa hesperia* Berry [7] and *N. knowltonii* Berry [5], but shows some slight differences in secondary venation and in the character of marginal teeth. The Kamchatkan species differs from the Middle Eocene North American *Nyssa californice* MacGinitie from the central Sierra Nevada [23] in the gradually tapering apex and secondary venation.

The new species is somewhat similar in its irregularly and coarsely dentate leaves to *Quercus gmelinii* Al. Br. which actually belongs to Nyssa [17]. Kvacek and Buzek have suggested that the latter species might be closely related to the extant *N. aquatica*. *N. budantsevii* has great variability of the leaf characters with the exception of the leaf shape, which is more or less constant (table 1). Among living species, the most suitable for comparison is *N. aquatica*, with gross-dentate leaves.

Occurrence. Western Kamchatka, Chemurnaut Bay, Evrava-veyem River; Kamchik (upper part) and Tkaprovayam formations, terminal Paleocene-Lower Eocene. Snatol River, Napana Formation, Upper Paleocene. Anadyrka River, terrigenous beds (upper part), Middle Eocene.

KEY TO PLATE II

Figs. 1-3 - *Nyssa budantsevii* sp. nov., western Kamchatka. 1 - Coll. 3736, No. 10A/75-24, Chemurnaut Bay, upper part of Kamchik Formation, Upper Paleocene. 2 - Coll. 3736, No. 6/87-24, Evrava-veyem River, upper part of Kamchik and/or lower part of Tkaprovayam formations, Upper Paleocene. 3 - Coll. 3858, No. 20A/75-13, terrigenous beds north of mouth of Anadyrka River, lower part of Middle Eocene. All figures ×0.8.

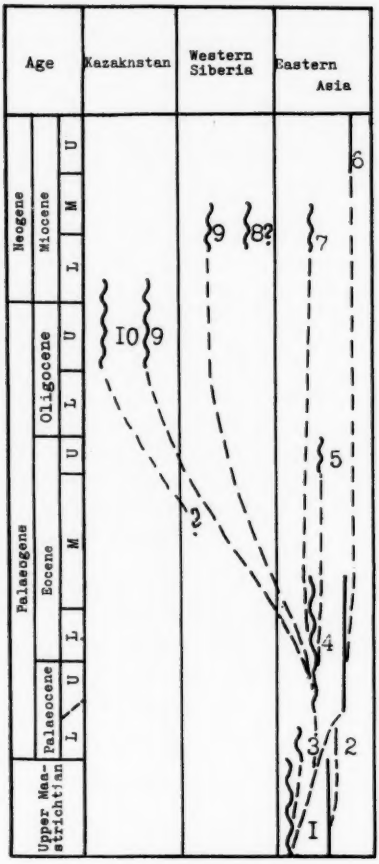

Fig. 6. Development of *Nyssa* species in the Cenozoic of Northern Asia. 1 - *N. tschucotica* Golovn.; 2 - *N. bureica* Krassil.; 3 - *N. tsagajanica* (Poyark.) Fotyan. comb. nov.; 4 - *N. budantsevii* sp. nov.; 5 - *N. komarovii* Ablaev et Akhmetev; 6 - *N. pseudoaquatica* Akhmetiev; 7 - *N. a-yokajamai* Tanai; 8 - *N. europaea* Ung., 9 - *N. alexeevii* (Poyark.) Fotyan., comb. nov.; 10 - *N. zhilinii* Vikulin et Pneva. } - serate-margined morphotype; | - entire-margined morphotype.

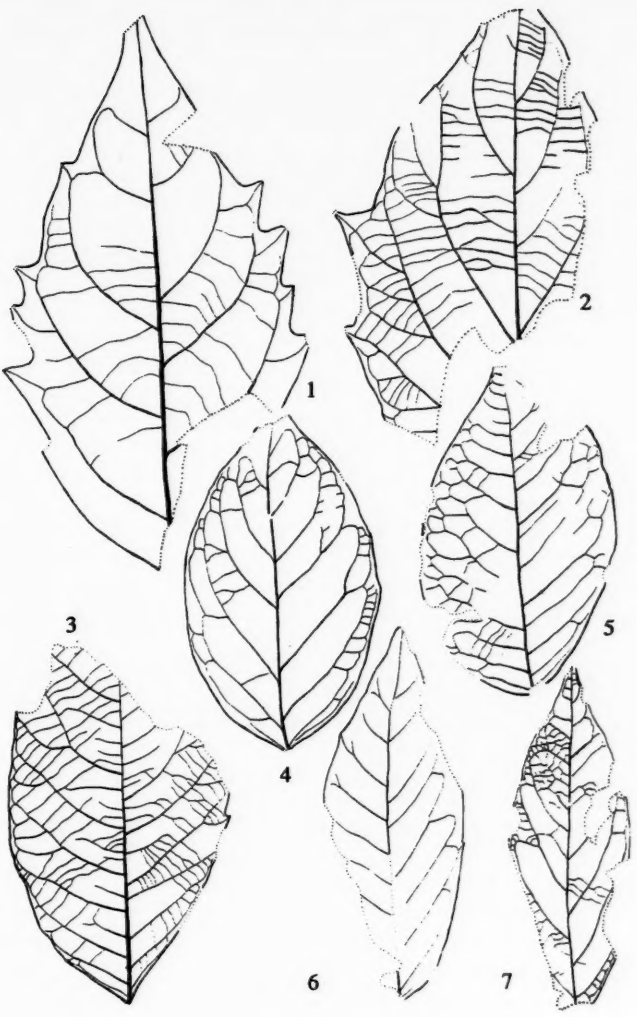

PLATE III

KEY TO PLATE III

Figs. 1-7 - *Nyssa budantsevii* sp. nov., western Kamchatka. 1 - Coll. 4256, No. 2/77-106b, holotype, Snatol River, Napana Formation, Upper Paleocene. 2, 3 - Coll. 3858. 2 - No. 20A/75-4; 3 - No. 20A/75-13, terrigenous beds north of mouth of Anadyrka River, lower part of Middle Eocene. 4, 7 - Coll. 3736. 4 - No. 6/87-21; 7 - No. 6/87-24, Evrava-veyem River, upper part of Kamchik and/or lower part of Tkaprovayam formations, Upper Paleocene. 5, 6 - Coll. 3736. 5 - No. 10A/75-24; 6 - No. 10/75-37, Chemurnaut Bay, upper part of Kamchik Formation, Upper Paleocene. All figures ×0.65.

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LIGNITIZED ENDOCARPS AND THEIR IMPRESSIONS OF *Nyssa sibirica* FROM THE LOWER MIOCENE OF NORTHERN KAZAKHSTAN

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Abstract. Lignitized endocarps of *Nyssa* and their impressions from the diatomaceous clays of the Lower Miocene in Borehole 338 west of Kustanay (Kazakhstan) have been investigated with light and electron scanning microscopes. The specimens are the combination of compressions and their impressions.

Форма сохранности плодов ниссы в виде лигнифицированных эндокарпов и их отпечатков позволяет выявить полный набор признаков, необходимых для обоснования видовой принадлежности.

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The extant genus *Nyssa* with its 7 species and the monotypic genus *Camtotheca* constitutes the family Nyssaceae. The genus *Nyssa* includes deciduous trees or shrubs native to eastern North America (*N. sylvatica* Marsh., *N. aquatica* L., *N. ogeche* Marsh., *N. biflora* Michx., *N. ursina* Small) and to southern and southeastern Asia (*N. sinensis* Oliv., *N. javanica* (Blume) Wang.). The fruits of American species *N. sylvatica, N. biflora, N. ursina* and Chinese *N. sinensis* are morphologically so similar that Eyde [6] suggested combining these species into "the *Nyssa* sylvatica complex."

Nyssa identified by fossil fruits have been known since the Early Eocene. There is fossil evidence that the former geographical distribution of the genus was wider than at present, and included North America, Europe, Siberia, and Japan [11]. According to Eyde and Barghoorn [7], it is possible to discern four morphological groups of *Nyssa* in the Paleogene of North America. These groups are related to the extant *N. aquatica, N. javanica, N. ogeche* and to the *N. sylvatica* complex. *Nyssa* species with close affinity only to *N. sylvatica* or more-or-less similar to *N. oqueche* [4, 8, 14, 15] existed from the Oligocene to Pliocene across Europe, Siberia and Japan. Until the 1960's, all fossil nyssaceous fruits and their imprints found within the former Soviet Union were traditionally named *N. disseminata* (R. Ludw.) Kirchh. Fossils of *N. disseminata* (the type is from Wetterau, Germany) were recorded from the Pliocene along the Duab River in western Transcaucasus [9, 10], from the Oligocene and Miocene of western Siberia [1, 2, 3, 11, 12],

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and from the Oligocene of Kazakhstan [13]. Later, Dorofeev [4] erected Asiatic species *N. sibirica* Dorof., *N. irtyshensis* Doror., and *N. macrocarpa* Dorof. (without the type designation) that he had earlier designated as *N. disseminata.** The first two species are similar to each other and to *N. disseminata*, with the major distinction being the number of locules. Fruits of *N. sibirica* and *N. irtyshensis* are always unilocular, while the Oligocene and Miocene fruits are bi- and multilocular [4]. The unilocular fruits of *N. disseminata* are reported only from the Pliocene [8]. Fruits of *N. macrocarpa* are very unusual; Dorofeev did not observe a close affinity of this species to any modern representatives of the genus. We have two Lower Miocene fruits of *Nyssa*, collected by S. G. Zhilin in Borehole 138 (Krugloe Lake, western Kustanay District), which were provisionally identified as *Nyssa* sp. [16]. Only one endocarp from two specimens of *Nyssa* is comparatively well preserved, but both fruits left sufficiently distinct imprints of their surface on diatomaceous clays.

Finds of *Nyssa* were reported earlier from the Tertiary of Kazakhstan: imprints of *N. disseminata* fruit from Ashutas [13] and a specimen of *Nyssa* sp. from near Bolattam [5]. However, endocarps of *Nyssa* and their imprints from the Krugloe Lake Borehole 138 are more closely related to the Miocene *Nyssa* from western Siberia — *N. sibirica* and *N. irtyshensis* — rather than to the earlier described fruits from Kazakhstan.

P. I. Dorofeev, the author of these species, indicated that fruits of *N. sibirica* are elliptical, 4.7-9.9 mm long and 2.0-5.0 mm wide with rounded or gradually narrowing base, rounded slightly pointed apex, and with narrow grooves running longitudinally over the surface. Although *N. irtyshensis* is very similar to *N. sibirica*, Dorofeev pointed out the greater length (7.9-10.0 mm) and smaller width (4.3-5.2 mm) of *N. irtyshensis*. Dorofeev also noted a slight distinction in their general shape: fruits of *N. sibirica* are slightly broader at the apex, while fruits of *N. irtyshensis* are somewhat narrower. Moreover, one fruit wall in *N. irtyshensis* is somewhat thicker, which, in Dorofeev's opinion, could be an indication of a reduction of the second locule.

Fruits found at Krugloe Lake have common morphological features with *N. sibirica*, although one wall, like in *N. irtyshensis*, is thicker. We examined several specimens of *N. sibirica* from Dorofeev's collection at the Department of Paleobotany (Komarov Bot. Inst.) and found

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*These species were published by the late Prof. Dorofeev [4] without designation of the type. This was corrected for *N. sibirica* by Zhilin, 1989, *The Bot. Rev.* 55 (4): 267. Thus, this species should be cited as *N. sibirica* Dorof. ex Zhilin.

Validation of two other species is given below:

Nyssa irtyshensis Dorof. sp. nov. - *N. irtyshensis* Dorof. 1963. *The Tertiary Floras of Western Siberia*. Moscow, Leningrad: 238 [sic], pl. 41, figs. 5-8, designat. typi omissa. Holotype: endocarp; Lower Miocene, Krasnoyarka village on the Irtysh River. (Dorofeev, ibid., pl. 41, fig. 7). For quotation: *N. irtyshensis* Dorof. ex Arbuzova et Zhilin.

N. macrocarpa Dorof. sp. nov. - *N. macrocarpa* Dorof. 1963. *The Tertiary Floras of Western Siberia*. Moscow, Leningrad: 239, pl. 41, figs. 9-19, designat. typi omissa. Holotype: endocarp; Oligocene, Nizhnyaya Pristan village on the Tavda River. (Dorofeev, ibid., pl. 41, fig. 13). For quotation: *N. macrocarpa* Dorof. ex Arbuzova et Zhilin.

PLATE I

that this thickening was also seen in *N. sibirica*. Therefore, *Nyssa* from Kazakhstan can be confidently identified as *N. sibirica*.

To study the structure of fruits of *N. sibirica* (Krugloe Lake) and of *N. sibirica* and *N. irtyshensis* (western Siberia) we embedded the specimens in epoxy resin and prepared microsection. We tried to cut sections, softened in HF acid, with a micotome, but the best results were obtained by polishing. Structure of fruit walls was examined also with the scanning microscope.

Nyssa sibirica Dorof. ex Zhilin

Pl. I, figs. 1, 2, 5-8; Pl. II, figs. 1-3; figs. 1, 2

N. sibirica Dorof. ex Zhilin 1989, *The Bot. Rev.* 55(4): 267, fig. 19 A, B. - *N. sibirica* Dorof. 1963, *The Tertiary Floras of Western Siberia*: 237, pl. 41, figs. 1-4; designat. typi omissa. *Nyssa* sp. Zhilin 1974, *The Tertiary Floras of the Ustyurt Plateau*: 63, pl. 49, figs. 5-8.

Holotype. Pl. 1, figs. 1, 2. Endocarp, Oligocene, Kozyulino village on the Tom River, western Siberia, Coll. 509 (Komarov Bot. Inst.); Dorofeev 1963, l.c.: 237, pl. 41, fig. 1.

Description. Endocarp (Coll. 1021, sample 1*a*) and impression are 8.1-13.9 mm long, 4.2-6.0 mm wide, and obovate; base and apex are rounded. Unilocular, triangular germination valves usually occupy somewhat less than half the length of endocarp. Surface bears 7 rounded longitudinal ridges with remains of vascular bundles in intervening grooves. Ventral face is slightly convex, dorsal face flat. Endocarp wall is 1.25-2.0 mm thick (thickest along dorsal side), composed of single inner layer of longitudinal sclereids surrounded by narrow zone of circumlocular fibers, and of outer region where aggregates of fibers run in many directions (pl. 2, fig. 3). Inner layer cells are not always clearly visible. Remains of mesocarp are observed as thin layer of thin-walled, equiaxial cells.

KEY TO PLATE I

Figs. 1, 2. *Nyssa sibirica* from Kozyulino (western Siberia), both sides of same endocarp, ×5.

Figs. 3, 4. *N. irtyshensis* from Krasnoyarka (western Siberia), both sides of same endocarp, 1 and 1A/1021, ×5.

Figs. 5, 6. *N. sibirica* from Lake Krugloe (Kazakhstan), impression of both sides of same endocarp, 1 and 1A/1021, ×5.

Figs. 7, 8. *N. sibirica* from Lake Krugloe (Kazakhstan), both sides of same endocarp (extracted from samples 1 and 1A/1021), 1a/1021, ×5.

Fig. 9. *N. sylvatica*, extant, endocarp.

All figures in reflected light.

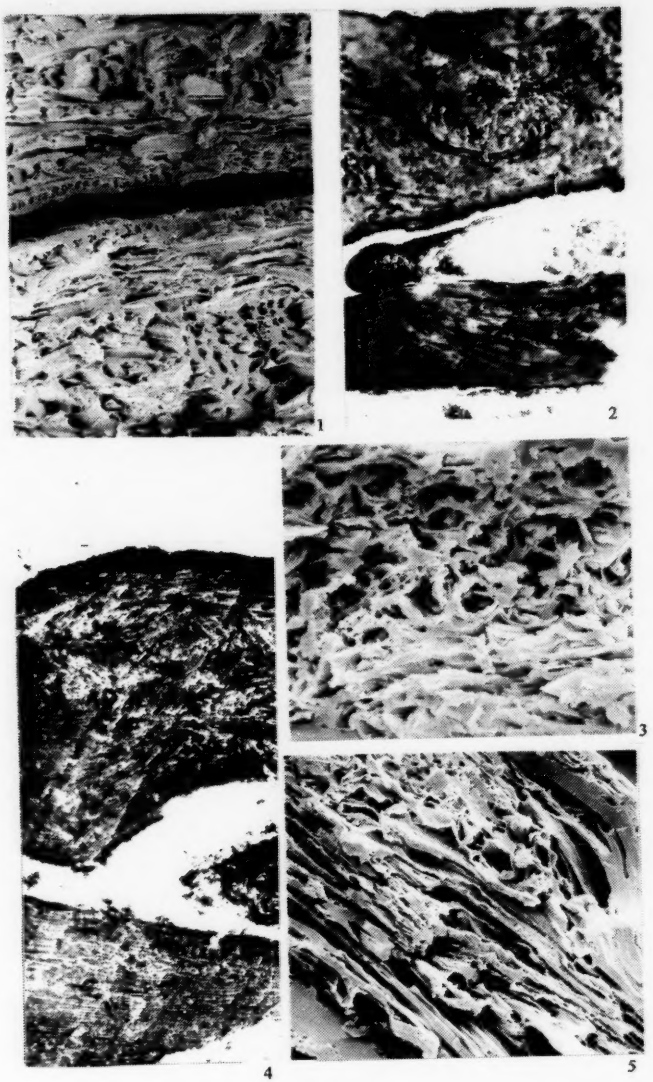

PLATE II

KEY TO PLATE II

Figs. 1, 2. Sections of *Nyssa sibirica* stone from Kozyulino (1 - ×300; 2 - ×400).
Fig. 3. Section of *N. sibirica* stone from Lake Krugloe, ×800.
Figs. 4, 5. Section of *N. irtyshensis* stone from Krasnoyarka (4 - ×400; 5 - ×500).
Figs. 2, 4. Reflected light micrographs; figs. 1, 3, 5 - SEM.

Fig. 1. *Nyssa sibirica* from Lake Krugloe, impression of endocarp (with fragment), 5/1020, ×4.

Fig. 2. *Nyssa sibirica* from Lake Krugloe; counter impression of endocarp (with its other fragment), 5A/1020, ×4.

Material. Two endocarps and their impressions; Krugloe Lake, Borehole 138, depths 142.0-171.8 and 137.8-141.8 m (Kustanay District, Kazakhstan), 1, 1A, 1a/1021 and 5, 5A/1020 (Komarov Bot. Inst., Department of Paleobotany).

Discussion. Anatomy of fruits of *Nyssa sibirica* from Kazakhstan and from western Siberia is, on the whole, similar (pl. 3, figs. 1-3).

The affinity of *N. sibirica* and *N. irtyshensis* to *N. complanata* from North America should be noted. Fruits of all these species are approximately equal in size, more-or-less elliptical, with narrow vascular bundles elongated across the endocarp surface (*N. sibirica* has 8-12 bundles, *N. irtyshensis* 6-8 bundles, and *N. complanata* 10-15 bundles). All these species are reported to have an inner layer of longitudinal fibers consisting of one row of cells and surrounded by a narrow zone of circumlocular fibers, and the outer region (pl. 2, figs. 1-5). Due to this similarity, *N. sibirica* seems to be closely related both to *N. irtyshensis* and *N. complanata*. Asiatic species differ from *N. complanata* only in the number of locules; *N. sibirica* and *N. irtyshensis* always have one locule, while *N. complanata* has 2-4 locules. Eyde and Barghoorn (1963) reported the close relationship of *N. complanata* to modern species of the *N. sylvatica* complex. Because of the similarity of the forms, no doubt remains about the affinity of fossil *N. irtyshensis* and *N. sibirica* to the extant *N. sylvatica* complex, especially to its American representatives which are always unilocular.

We have both the fruits and their imprints for our studies. External morphology of the endocarp (size, pattern of vascular system, presence and size of valve) is clearly reflected in the imprints. When such imprints are available, the age of deposits is known, and the fossil locality

is accurately known, then the assignment of imprints can be made at the species level with confidence; however, it is sometimes doubtful whether this imprint was left by a fruit of *Nyssa* or some other species with a different number of locules and unusual inner structure.

The imprints of *Nyssa* sp. from Mynsualmas [16] should be assigned to *N. ornithobroma* Ung. [14] on the basis of the large size of the imprint and its elliptical shape.

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Firmiana (STERCULIACEAE) FROM THE UPPER EOCENE OF WESTERN KAMCHATKA

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Abstract. *Firmiana kovatschensis* Budants et M. Baranova, n. sp. (Sterculiaceae) is described from marine Upper Eocene deposits in midstream of the Napana River (western Kamchatka). The species is found in a plant assemblage, somewhat unusual for a temperate flora in this region. In morphology and epidermal structure, the fossil leaves are similar to some extant species of *Firmiana*. This new find is one of the oldest and northernmost occurrences of this genus.

Новый вид *Firmiana kuratschenensis* происходит из верхне-эоценовых отложений среднего течения р. Напана, западная Камчатка. Он обнаружен в комплексе, необычном для умеренных флор этого региона. По морфологии и эпидермальным признакам ископаемых вид сходен с некоторыми современными видами фирмианы. Это самая древняя и самая северня находка рода.

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On our field trips in 1983 and 1984 to the Napana River basin in western Kamchatka, we made a fossil plant collection that was unusual in its systematic composition. A new extinct species, *Firmiana kovatschensis* Budants. et M. Baranova, whose leaf impressions are described below, was found in this assemblage.

Numerous plant remains occurred in three localities on the Napana River banks below Sedanka village. The outcrops are of fine-layered, thick, light gray clays with occasional large siliceous siderite concretions 2-2.5 m in diameter; some outcrops contain abundant leaf impressions, mollusks and benthic foraminifera. The deposits are referred to the marine Kavacha Formation, and are reliably dated as Late Eocene.

The Napana locality represents a unique case of mass burial of land plants in marine strata which, based on the marine fauna composition, are not coastal facies. This probably results in a certain artificial sorting of plants due to selective preservation of thick and coriaceous leaves that are capable of a long stay and transport in sea water. Therefore, thin chartaceous leaves are rarely found where needle-bearingshoots of conifers and coriaceous angiosperm leaves dominate. The marine origin of the assemblage is also indicated by narrow linear leaves of "sea grass" *Zostera* or *Posidonia* type, and algae thalli similar in morphology to some extant species of *Enteromorpha*.

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Fig. 1. *Firmiana kovatschensis* sp. nov., holotype, BIN No. 960-29/2556.

The Sedanka assemblage of fossil plants comprises on the whole the following taxa: *Araucaria dubia* Budants., *Abies tigilensis* Cheleb., *Pinus kovatschensis* Budants., *Picea sp.*, *Sequoia affinis* Lesq., *Metasequoia occidentalis* (Newb.) Chaney, *Glyptostrobus europaeus* (Brongn.) Heer, *Cunninghamia sinelnikoviae* Cheleb., *Thuites napanensis* Budants., *Magnolia praekobus* Budants., *Laurophyllum sp.*, *Fagus napanensis* Fotyan., *Betula sp.*, *Juglans pogojevii* Cheleb., *Rhododendron mainachense* (Cheleb.) Budants., *Tilla sp.*, *Firmiana kovatschensis* Budants. et M. Baranova, *Euphorbiophyllum erodofolium* Budants., *Leguminosites sp.*, *Kolreuteria kamtschatica* Budants., *Ceanothus rectinervis* Budants. and *Macclinotockia kovatschensis* Budants. Some impressions of angiosperm leaves have not yet been identified.

Development of the paleoflora of the Sedanka assemblage was preceded by a flora essentially different in systematic composition and by dominance of the thermophilic component; the latter included palms, lauraceous and myrtaceous leaves, numerous legumes, and other angiosperm taxa. They were "exotics" in northeastern Asia during the Paleogene (Fotyanova, 1989; Budantsev, 1989). The Sedanka assemblage represents the beginning of a new stage in the history of the Paleogene flora of western Kamchatka. The flora again became temperate or warm-temperate during the late Eocene, and retained occasional thermophilic plants to which *Firmiana kovatschensis* seems to belong. Description of this taxon is below.

Sterculiaceae

Firmiana Marsigli

Firmiana kovatschensis Budants. et M. Baranova sp. nov.

Figs. 1 and 2; fig. 3-1-3; fig. 4-1, 2

Holotype. Leaf impression, Upper Eocene, western Kamchatka, Napana River. Botanical Institute, St. Petersburg, No. 960-29/2556, fig. 1.

Description. Leaves are petiolate, palmate-trilobate, sometimes longitudinally asymmetrical, 8-13 cm long (without petiole), 9-13 cm wide in median part. Assymetry is expressed either in the length and breadth of later lobes, or in underdevelopment of one lobe as shown by the different angles of divergence of the lateral veins (fig. 3-1, 2). Petioles are thick, considerably exceeding basal veins in thickness. Margin is entire, slightly revolute due to thickening; blade texture is thick, and coriaceous. Central lobes are longer than lateral ones, slightly constricted at base, convex laterally, and rounded-acuminate at apex. Lateral lobes widen distally, and also have convex sides and rounded-acuminate apices. Sinuses between lobes are rounded, and of various depths. Lamina base is rounded or slightly auriculate.

Venation is palmate craspedodromous: central and lateral basal veins diverge from enlarged node or, in the case of lamina asymmetry, are at different levels (fig. 3-1, 2). The central and lateral basal veins of internal pair are thick, gradually thinning at the base and terminating in the lobe apex. Veins of the external pair are thin, rapidly joining external branches of the next pair of veins. Secondary (lateral) veins are very thin, semi-submerged in the blade tissue, diverging at 60 degrees, and joining by wide loops near the margin. Tertiary veins form a rather loose network of sinuous anastomoses. The mesh is filled with a thin network of more-or-less rounded closed areolae.

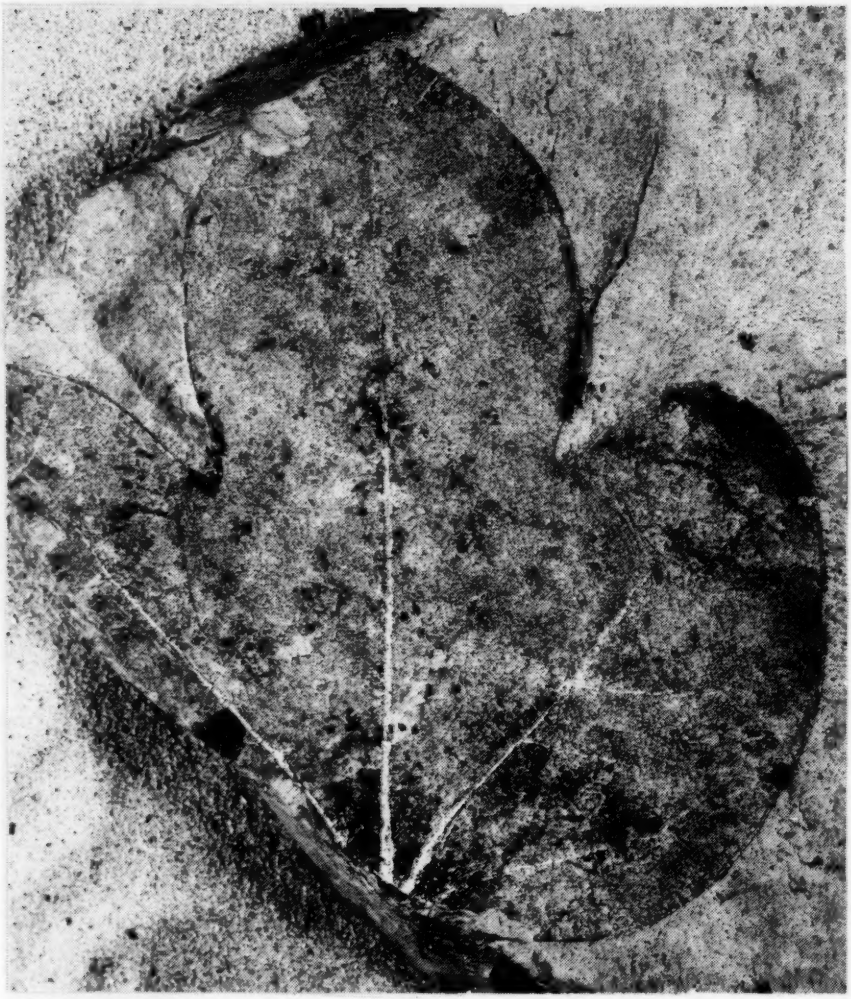

Fig. 2. *Firmiana kovatschensis* sp. nov., BIN No. 960-29/2566.

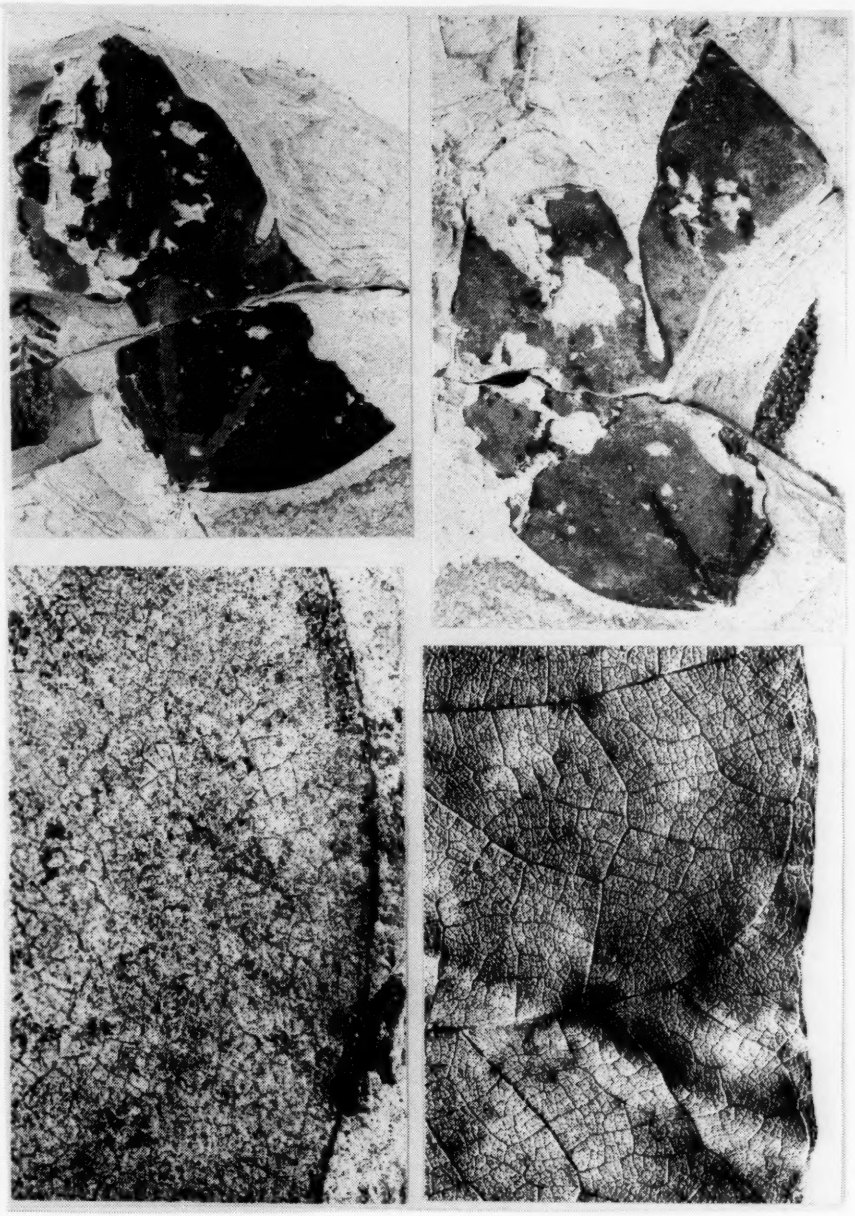

Fig. 3. 1-3 - *Firmiana kovatschensis* sp. nov.: 1 - leaf impression with phytoleima; 2 - its opposite imprint, BIN No. 960-29/2598; 3 - detail of leaf lamina, ×3, BIN No. 960-29/2566; 4 - *Firmiana diversifolia* A. Gray (Recent), detail of leaf, ×3. LE, A. C. Smith 7059.

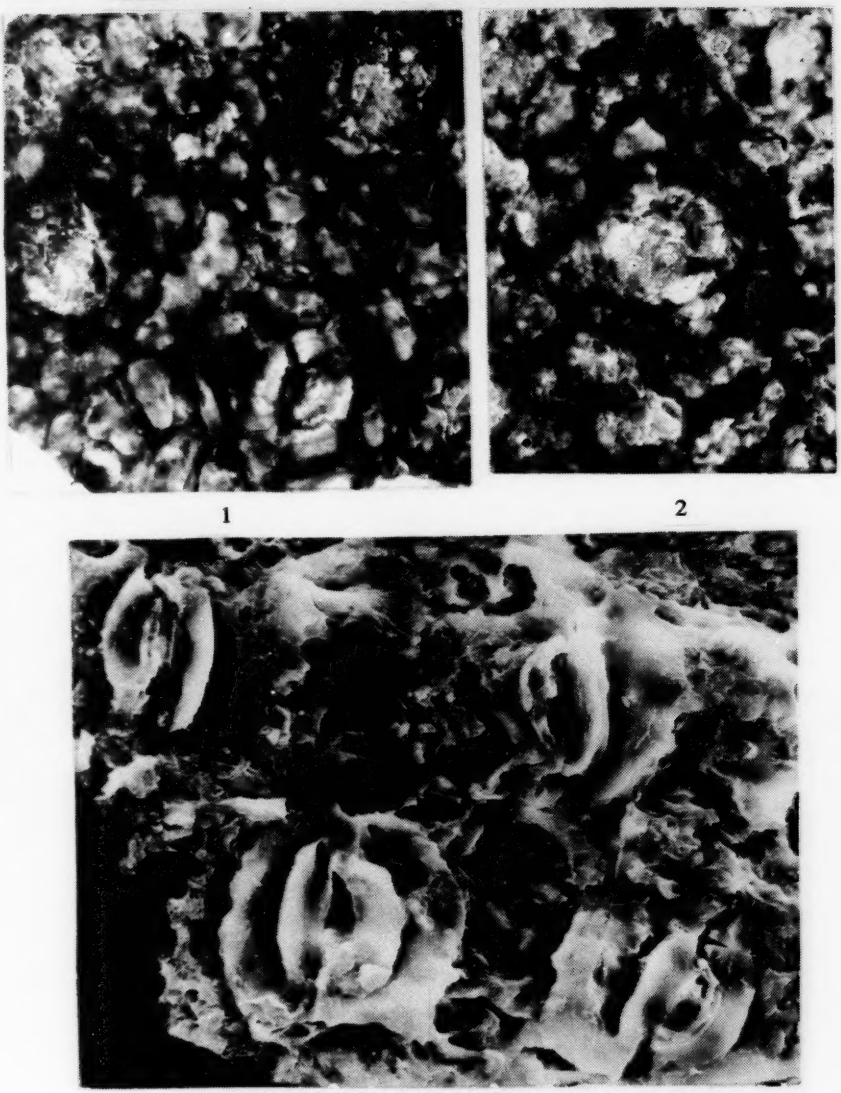

Fig. 4. 1, 2 - *Firmiana kovatschensis* sp. nov. Epidermal structure of leaf, ×400. BIN No. 960-29/2598; 3 - *Firmiana diversifolia* A. Gray (Recent), epidermal structure of leaf, ×600. LE, A. Smith 7059.

One specimen is a coaly compression which allowed study of the leaf cuticle structure (figs. 3-1; 4-1, 2). Epidermal cells are small, polygonal, with straight or slightly curved thickened anticlinal walls. Stomata are large, 42-57 × 30-51 μm, surrounded by several subsidiary cells (presumably 4-6). Stomata are close to each other due to small epidermal cells. Guard cells of the stomata have well-developed thick ledges and strongly cutinized epidermal walls. Surrounding cells form a peristomatal ring. Multicelled trichome base present.

Discussion. There is an obvious similarity in epidermal structure with an extant species, *Firmiana diversifolia* A. Gray, whose epidermal cells are also small, polygonal with straight or slightly curved, thickened anticlinal walls (fig. 4-3). Stomata are, however, smaller, 21-24 × 18-21 μm, surrounded by 4-6 subsidiary cells. Stomata are anomocytic, intermediary between anomocytic and encyclocytic or stephanocytic, tetracytic or staurocytic. Walls of stomata surrounding cells are straight or slightly curved and thickened. Stomata are dense; guard cells have well-developed external projections and thickened cutinized outer walls. Stellar trichomes are numerous with multicelled base. Stomata of fossil leaves are more than twice the size of the modern species.

The Kamchatkan species displays certain superficial similarity in leaf morphology with *Firmiana diversifolia*, but especially with another extant species, *F. platanifolia* (L.) Schott et Endl., a deciduous tree in forests of China and Japan. Leaves of the latter species vary widely in shape and size, from entire to 3-5 palmate-lobate; lobe shape ranges from attenuate-triangular to convex-rounded with acute or attenuate-acuminate apices. Lamina base can be deeply cordate, auriculate or, rarely, rounded. Typical are the long, strong petioles that form thick nodes at the junction with the leaf blade where thick basal veins diverge. Similarity is also observed in the venation patterns of the second and higher orders. In both extant species, secondary veins are joined by wide loops near the lamina margin, and external branching forms a second row of small loops, almost fused with the thickened margin (fig. 3-4). As in the fossil species, tertiary veins form a loose network of rounded or angular closed areolae (fig. 3-3). However, the epidermal structure of *F. platanifolia* differs from that of the fossil species.

A. N. Kryshtofovich (1916) was one of the first who indicated the possible occurrence of *Firmiana* in fossil floras, assigning impressions of lobate leaves from the Miocene of the Krynka River to this genus. He compared them to the earlier described species, *Dombeyopsis tridens* Ludwig (Ludwig, 1860), from the Early Miocene of Salzhausen, Germany, and suggested a new combination—*Firmiana tridens* (Ludwig) Krysht. Later, this species was indicated for a number of other Neogene floras from the Ukraine and European Russia (Iljinskaja, 1968). *F. platanifolia* (*F. simplex* W. F. Wight, pro syn.) is also given as a modern analogue of this fossil species. We should mention a certain similarity of the Kamchatka leaves to those from Europe in leaf morphology and type of venation, although the latter leaves differ by shorter and wider lobes with rounded sinuses and deeply cordate lamina base.

Among the Asian fossils, we note first of all, *F. sinomiocenica* Hu et Chaney, from the Miocene flora of Shantung province in northeastern China (Hu and Chaney, 1940). Leaves and fruits of this species are very similar to those of modern *F. platanifolia*. Leaves of the Chinese species are, unlike those from Kamchatka, deeply cordate at the base, and have three pairs of basal veins. The central lobe is slightly constricted at the base and the lateral lobes have wider external sides. Fragments of leaves with strong petioles are described from the Miocene of Mamontova Gora, Aldan River, in Yakutia as *Firmiana sp.* and are also compared with extant *F. platanifolia* (Iljinskaja and Schvareva, 1976). N. Ya. Schvareva indicates that similar and more

complete leaf impressions of *Firmiana* from the Miocene at Kavavlya River in Central Kamchatka are in A. I. Chelebaeva's collection. This, however, needs further verification.

Three to five-lobate leaves from Paleogene floras in western and, especially, southeastern United States are assigned to different species of *Sterculia*; some of them could well belong to extinct species of *Firmiana*. However, no leaves have been found that are closely comparable to our new species.

Therefore, *F. kovatschensis* can be considered the most ancient northernmost find of this genus in Asia.

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Liquidambar L. FROM THE CENOZOIC OF EASTERN ASIA

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Abstract. Cenozoic Far East records of *Liquidambar* are reviewed. In Sakhalin and Kamchatka this genus ranges from the Late Paleocene to Miocene. Most fossil leaf species fall in the range of morphological variation of two species: *L. miosinica* Hu et Chaney and *L. pachyphylla* Knowlton.

Приведен обзор местонахождений *Liquidambar* в материковой части Дальнего Востока и на Японских островах. Рассмотрено историческое развитие рода в течения палеогена и неогена. Описанные в литературе виды укладываются в пределы двух параллельно развивавшихся групп, различимых по морфологии и эпидермальному строению листьев.

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Introduction

Liquidambar is one of the most common components of the Cenozoic floras of the northern hemisphere. It could be a widespread genus of the broadleaved warm-temperature deciduous forests. The disjunct extant ranges demonstrate the great antiquity of this genus. In the Russian Far East *Liquidambar* occurred continuously from the latest Paleocene to the Middle Miocene.

The species composition of extant *Liquidambar* is disputable. According to G. Depape [11], *Liquidambar* is monotypic with the single species *L. styraciflua* L. The variable morphology of its leaves depends mainly on environmental conditions and developmental stages. Other authors recognize three or even more species [31]. The three most commonly recognized species are *L. styraciflua, L. orientalis* Mill, and *L. formosana* Hance, occurring locally in North America, Asia Minor, Taiwan, and mainland China.

The main reason for the taxonomic controversy on the fossils of the genus is the extremely variable leaf morphology. According to Z. I. Makarova [23], none of the generally used characters—number, size and shape of lobes, base and apex configurations, marginal serrations—appear to be species specific. Therefore, I conclude that most of the fossil species of *Liquidambar* are not valid.

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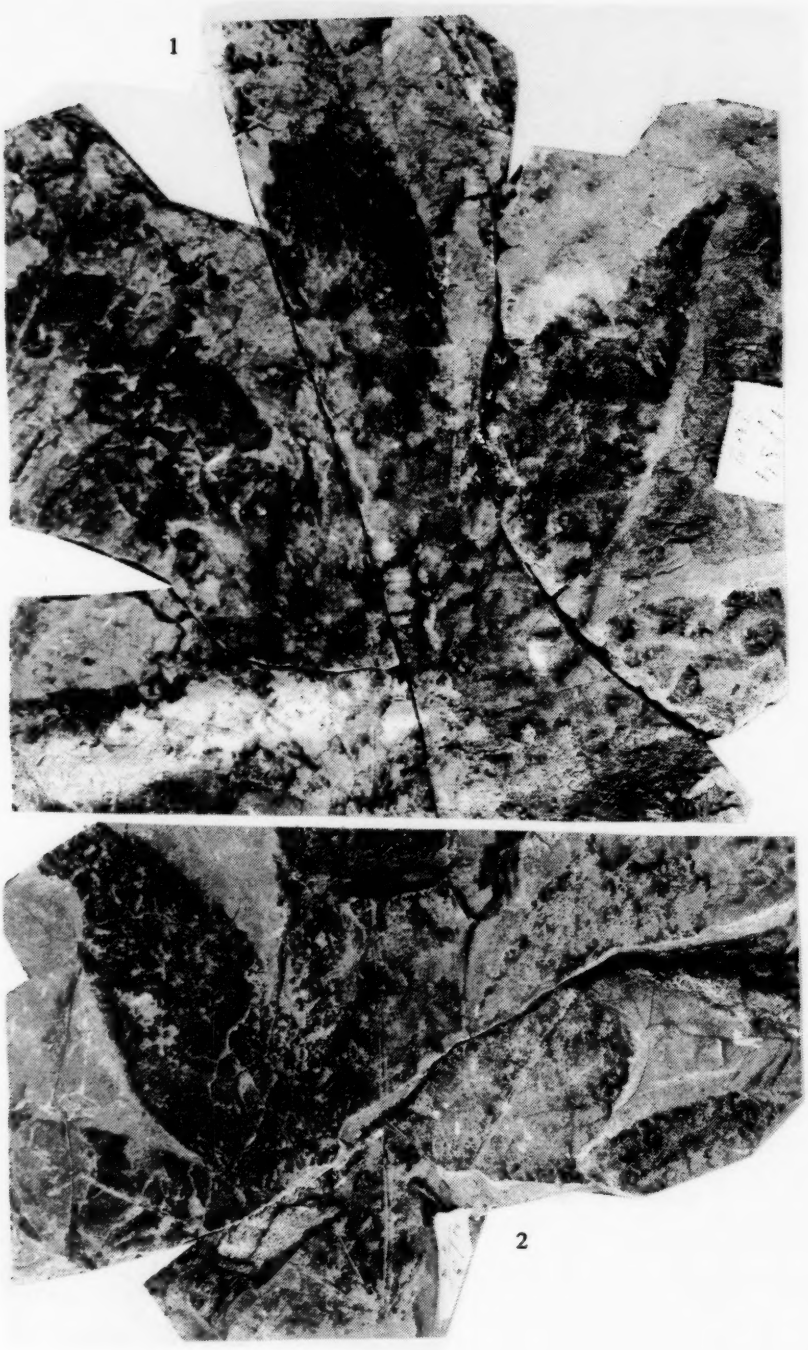


PLATE I

Cenozoic records of the genus *Liquidambar* are leaves and, rarely, reproductive organs, and a few epidermal structures [1].

Review of Macrofossil Records

T. Tanai and N. Suzuki [29] systematized *Liquidambar* records from Japan. They have combined under *L. miosinica* several species described by Hu and Chaney [16] from the Miocene Shanwang flora of China. They considered this species as closely related to the extant *L. formosana*. *L. miosinica* is similar to the extinct species *L. californicum* Lesq. and *L. pachyphylla* [16]. Subsequent research has enlarged the morphological characteristics of *L. miosinica* [25, 26, 29, et al.]. *L. mioformosana* Tanai [27] from the Middle Miocene Kamigo Formation was later included in *L. miosinica* [29]. The assignment of the Miocene *Liquidambar* from Japan to the extant *L. formosana* [13, 24, et al.] was questioned by Tanai and Suzuki [29], who regarded these fossils as *L. miosinica*.

L. protopalmata (K. Suzuki) Uemura from the Late Miocene Takamine Formation of northeast Honshu, Japan [31], is very similar to *L. pachyphylla*, first described from Van Horn's locality, the Mascall beds in Oregon [20]. *L. yabei* (Morita) Huzioka from the Middle Miocene Daibo Flora, Japan [18], has the same morphology.

Liquidambar is more common and diverse in Japan than in the adjacent continental eastern and northeastern Asia (fig. 1), ranging from the Middle Eocene to Pliocene [28]. Incidentally, *L. protoformosana* Endo var. *eocenica* Endo from the Middle Eocene Woodwardia beds [12] is very similar to *L. cordata* (K. Suzuki) Uemura [31] from the Late Miocene Takamine Formation.

L. miosinica is most common in the Daijima-type floras. It is known from the Middle Miocene Shimonoseki Formation, southwest Honshu, and the Middle Miocene Daibo Flora, western Honshu.

L. miosinica was recorded from the Middle Miocene of Korea on the continent [2, 3, 17].

Liquidambar first appears in the Late Eocene Bolotnaya Flora [22] in the Primor'ye Region of Russia. *L. miosinica* is common in the Nadezhdinskaya Formation of the Rechnoy Peninsula [21], and also is from the Miocene of the Abramovka River and Kraskino [1, 3].

L. europeae Al. Br. was reported from the Eocene Konglomeratnaya Formation on the Onor River [8] in Sakhalin. It is, however, indistinguishable from *L. miosinica*.

KEY TO PLATE I

Figs. 1, 2. *Liquidambar pachyphylla* Knowlton. 1 - Coll. 4129, No. 4/84-209, leaf impression, eastern Sakhalin, Bogataya River; 2 - Coll. 4129, No. 4/84-78, leaf impression, eastern Sakhalin, Bogataya River.

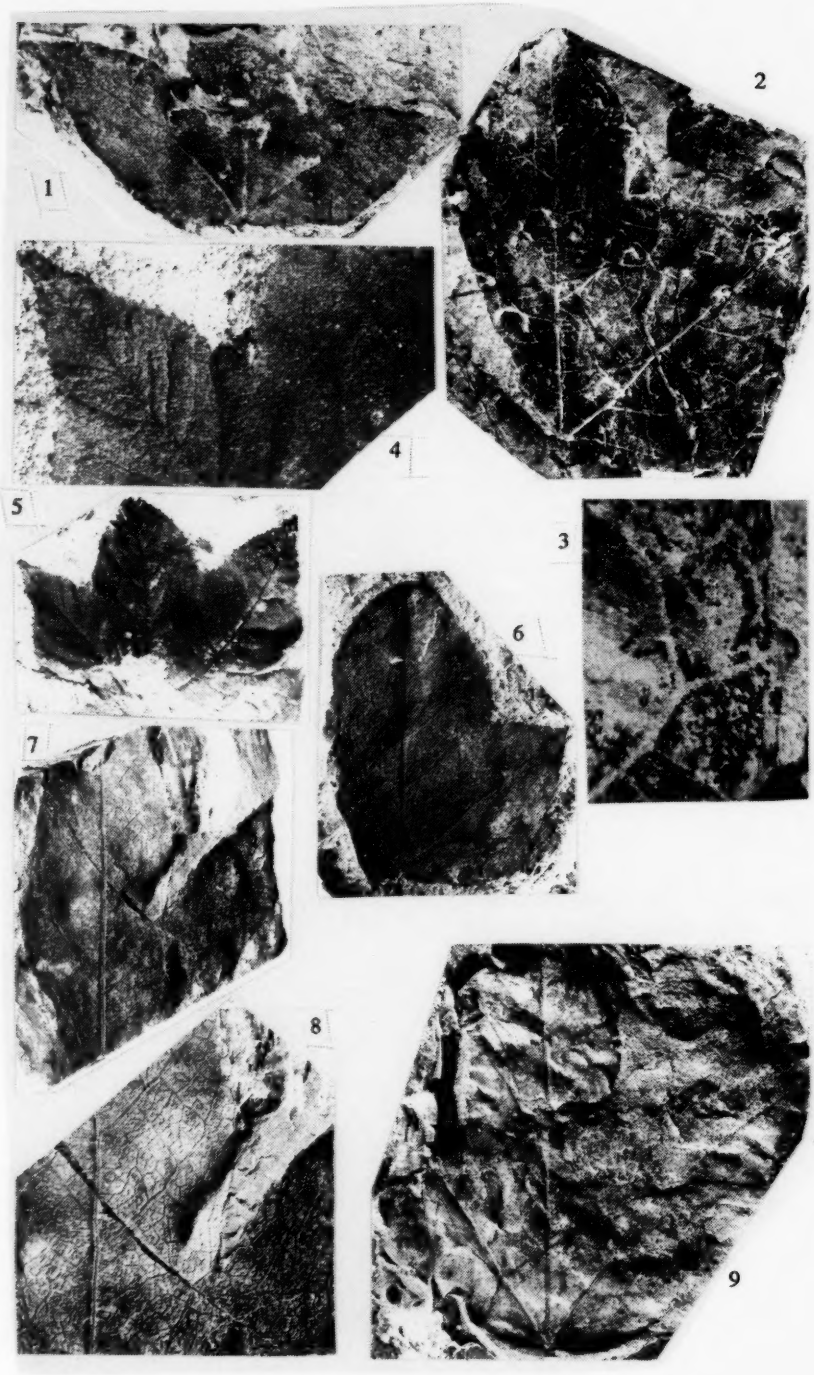


PLATE II

I studied *L. miosinica* from a number of Middle Miocene localities in western Sakhalin: Kama, Snezhinka, Aralskaya, Krasnoyarka and Naiba rivers, and from a single locality on the Korallovka River. *L. pachyphylla* was collected from a single locality in eastern Sakhalin—the Bogataya River, which was preliminarily assigned to the upper Middle to Upper Eocene (fig. 2).

A new species, *L. kamchatica* Cheleb., was described from the Middle Eocene of the Snatol River [10] in Kamchatka. In this species the leaf lobes are basally constricted while the marginal teeth are irregular and widely spaced. These features are rather atypical for *Liquidambar*, and suggests araliaceous or sterculiaceous affinities of the Snatol leaves.

I studied numerous leaves of *L. miosinica* from the Upper Eocene Irgirni Formation, Podkagernaya Bay, western Kamchatka. A single specimen of *L. miosinica* from the terminal Paleocene-Lower Eocene Tkaprovayamskaya Formation of Chemurnaut Bay, western Kamchatka, is the oldest record of *Liquidambar* in the Russian Far East (fig. 2).

This review indicates that the Far East *Liquidambar* leaves fall into two distinct groups: The first is the "*L. miosinica* group," including *L. miosinica*, *L. mioformosana*, *L. mioformosana* var. *cordata*, and *L. cordata*. The second, "*L. pachyphylla* group," consists of *L. pachyphylla*, *L. protopalmata* and *L. yabei*. They differ mostly in the shape of the leaf lobes (short, triangular, typically broad at the base in *L. miosinica*, narrow oblong in *L. pachyphylla*), the number of secondaries (about 6-8 pairs in *L. miosinica*, 8-10 pairs in *L. pachyphylla*), and the marginal serration (larger acuminate teeth in *L. pachyphylla*). It is possible that these groups correspond to two extinct species of *Liquidambar*.

Family **Altingiaceae** Lindley

Genus ***Liquidambar*** L.

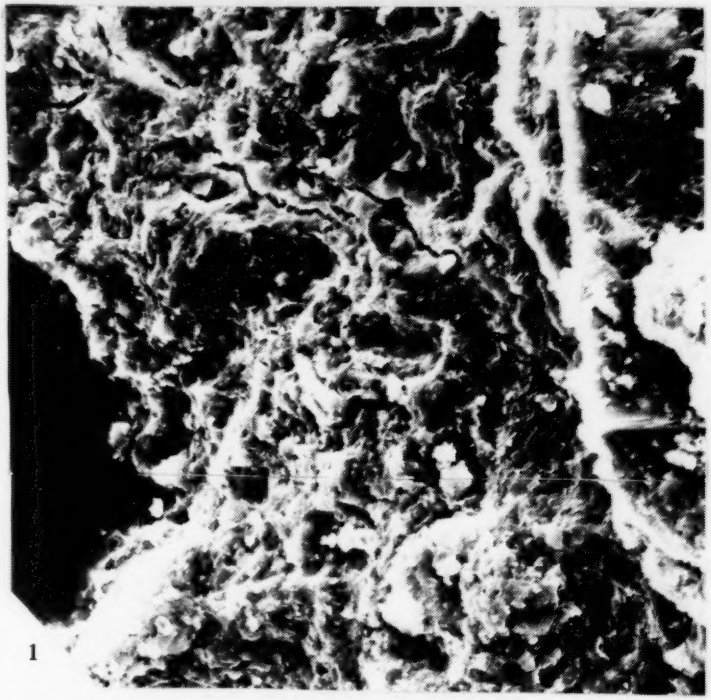
Liquidambar miosinica Hu et Chaney

(Pl. II, figs. 1-9; fig. 2: 1-6, 8-10, 12)

Holotype. No. 205, Nat. Geol. Surv. of China; almost complete leaf impression; China, Shantung Province, Upper Miocene; Hu et Chaney, 1940, p. 46, pl. 23, fig. 2.

KEY TO PLATE II

Figs. 1-9. *Liquidambar miosinica* Hu et Chaney. 1 - Coll. 4253, No. 1/84-22a, leaf impression, western Sakhalin, Naiba River; 2 - Coll. 3736, No. 3736/6A/2, leaf impression, western Kamchatka, Chemurnaut Bay; 3 - Coll. 3736, No. 3736/6A-2, the teeth, (×10), western Kamchatka, Chemurnaut Bay; 4 - Coll. 4252, No. 15H/74-1, the lateral lobe, (×3), western Sakhalin, Krasnoyarka River; 5 - Coll. 4252, No. 15H/74-1, leaf impression, western Sakhalin, Krasnoyarka River; 6 - Coll. 3862a, No. 4/85-4, leaf impression, western Kamchatka, Podkagernaya Bay; 7 - Coll. 3862a, No. 1b/3-79, leaf impression, western Kamchatka, Podkagernaya Bay; 8 - Coll. 3862a, No. 1b/3-79, leaf impression, (×2), western Kamchatka, Podkagernaya Bay; 9 - Coll. 4448, No. 3/90-227a, leaf impression, western Sakhalin, Kama River.



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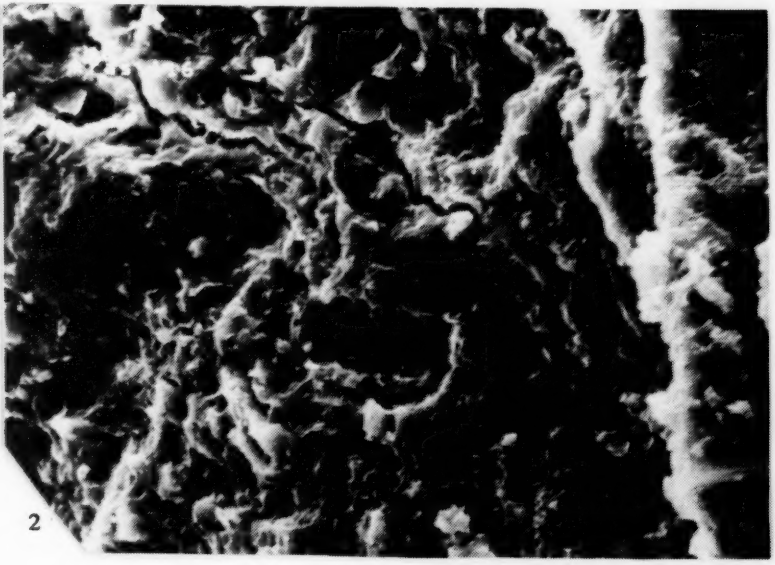

2

PLATE III

Material. Twenty-eight leaf impressions from western Kamchatka (Chemurnaut and Podkagernaya bays) and western Sakhalin (Kama, Snezhinka, Aralskaya, Krasnoyarka, Naiba, and Korallovka rivers).

Description. Leaf blade is medium-sized, symmetrical, palmately 3-5-lobed; lobes are triangular at base, their apex is acuminate. Central lobe is larger than the others. Sinuses between lobes are acute or rectangular. Base of lamina is broadly rounded, slightly cordate. Venation is marginal actinodromous. Midrib is straight, basal veins are mainly recurved. Secondary veins are thin, 6 pairs or more, forming series of loops near margin. Margin is finely serrate throughout, teeth are short and stout, glandular.

Discussion. This species has extremely variable leaves. Hu and Chaney described 3-lobed leaves, but later 5-lobed leaves have been also assigned to *L. miosinica*. The typical morphotype is similar to extant *L. formosana*. One impression of *L. miosinica* from Chemurnaut Bay (western Kamchatka) is very unusual, having straight basal veins and angular loops. Notably, this is the oldest record of the genus in the Far East.

Occurrence. Uppermost Paleocene: western Kamchatka, Chemurnaut Bay, Tkaprovayamskaya Formation. Middle Eocene: western Sakhalin, Kama, Snezhinka, and Aralskaya rivers, Snezhinkaskaya Formation; Krasnoyarka, Naiba River, Lower Due Formation. Upper Eocene: Kamchatka, Podkagernaya Bay, Irgirni Formation. Upper Lower-lower Middle Miocene: western Sakhalin, Korallovka River, Upper Due Formation.

Liquidambar pachyphylla Knowlton

(Pl. I, figs. 1, 2; fig. 2: 7, 11)

Lectotype. No. 8534; National Museum, Washington, D.C., USA; 5-lobed leaf without central lobe; Oregon, John Day Basin, Mascall beds, Middle Miocene; Knowlton, 1902; pl. 9, fig. 1.

Material. Two almost complete impressions and 7 leaf fragments from Bogataya River, eastern Sakhalin.

Description. Leaves are variable in size, symmetrical, typically palmately 5-lobed. Lobes are ovate, ovate-lanceolate, oblong. Lobe margins are parallel, distally tapering to a pointed apex. Sinuses between lobes are acute. Base of lamina is rounded, slightly cordate. Venation

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KEY TO PLATE III

Liquidambar pachyphylla Knowlton, epidermal structures seen on leaf impression: 1 - stomata and a hair base (arrow); lower stoma showing guard cells, those above it showing stomatal pits surrounded by narrow circle of subsidiary cells; SEM, ×1000; 2 - two adjacent stomata, SEM, ×1700.

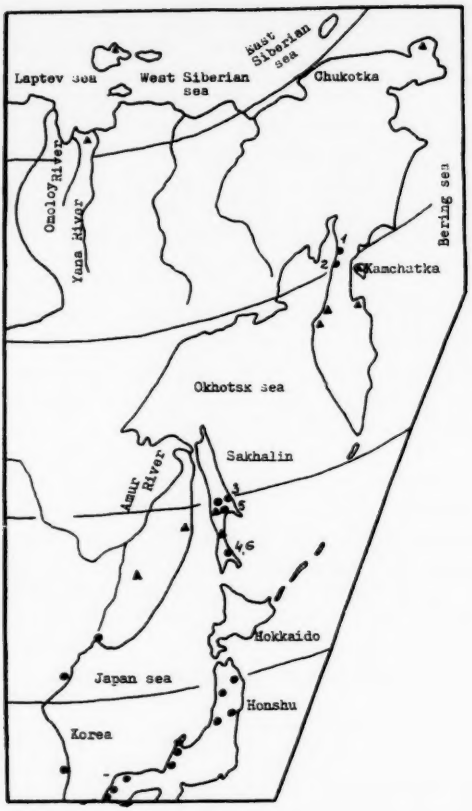


Fig. 1. Localities of fossil *Liquidambar* in eastern and northeastern Asia: 1-6 - localities where original material was collected; 1, 2 - western Kamchatka: 1 - Chemurnaut Bay; 2 - Podkagernaya Bay; 3 - eastern Sakhalin, Bogataya River; 4-6 - western Sakhalin: 4 - Naiba River; 5 - Kama, Snezhinka, Aralskaya rivers; 6 - Krasnoyarka River. ● - leaf impressions; ▲ - pollen grains.

is marginal actinodromous. Primary vein is straight, basal veins diverge from one point of base, are of equal thickness. There are about 8-10 pairs of secondary veins, thin, forming large loops near margin. Margin is regularly serrate throughout, teeth are large.

Discussion. This species is characterized by 5-lobed leaves with narrow oblong lobes. The marginal teeth are larger than in *L. miosinica*. *L. pachyphylla* closely resembles *L. protopalmata* and *L. yabei*. Among modern species, *L. pachyphylla* is comparable with *L. styraciflua*.

Occurrence. Upper Middle Eocene? - Upper Eocene. Eastern Sakhalin, Bogataya River, Lukamenskaya Formation.

Epidermal Structures and Pollen

A few fragments of the leaf impression of *L. pachyphylla* show stomata and hair bases (pl. III). The stomata pit is rounded-elliptical, 14.0 mm long, exposing most of the guard cells with broad lateral thickenings, which are surrounded by a circle of subsidiary cells smaller than the ordinary epidermal cells, occasionally showing transverse striation.

The hair bases are small, rounded, and surrounded by radially disposed cells with slightly concave radial walls. The hair bases are adjacent to the stomata.

Among extant species, *L. styraciflua* has moderately dense stomata (almost twice as dense as in *L. orientalis*, but much less dense than *L. formosana*); whereas occasional adjacent stomata share a subsidiary cell, contiguous stomata regularly occur in *L. formosana*. The stomata are described as paracytic but the lateral subsidiary cells in most cases are not distinct from other radially oriented peristomatal cells [23].

My species is similar to *L. styraciflua* in the frequency of stomata and of stomata sharing a subsidiary cell. Stomata are more numerous than in Miocene species *L. europea* [23].

An occasional pollen grain sticking to the leaf surface (fig. 3) is elliptical in equatorial outline, 18.0 mm long, 14.6 mm broad, showing pores as inconspicuous pits along the periphery.

Palynological Record

Liquidambar pollen first appears in the Lower Eocene Tastakhskaya Formation [5]. The Eocene range of the genus embraced the territories between the Yana and Omoloy rivers [5] as well as northern Chukotka [4]. The most northern record in northeastern Asia is from the Anzuskaya Formation, Faddeyevskiy Island [15].

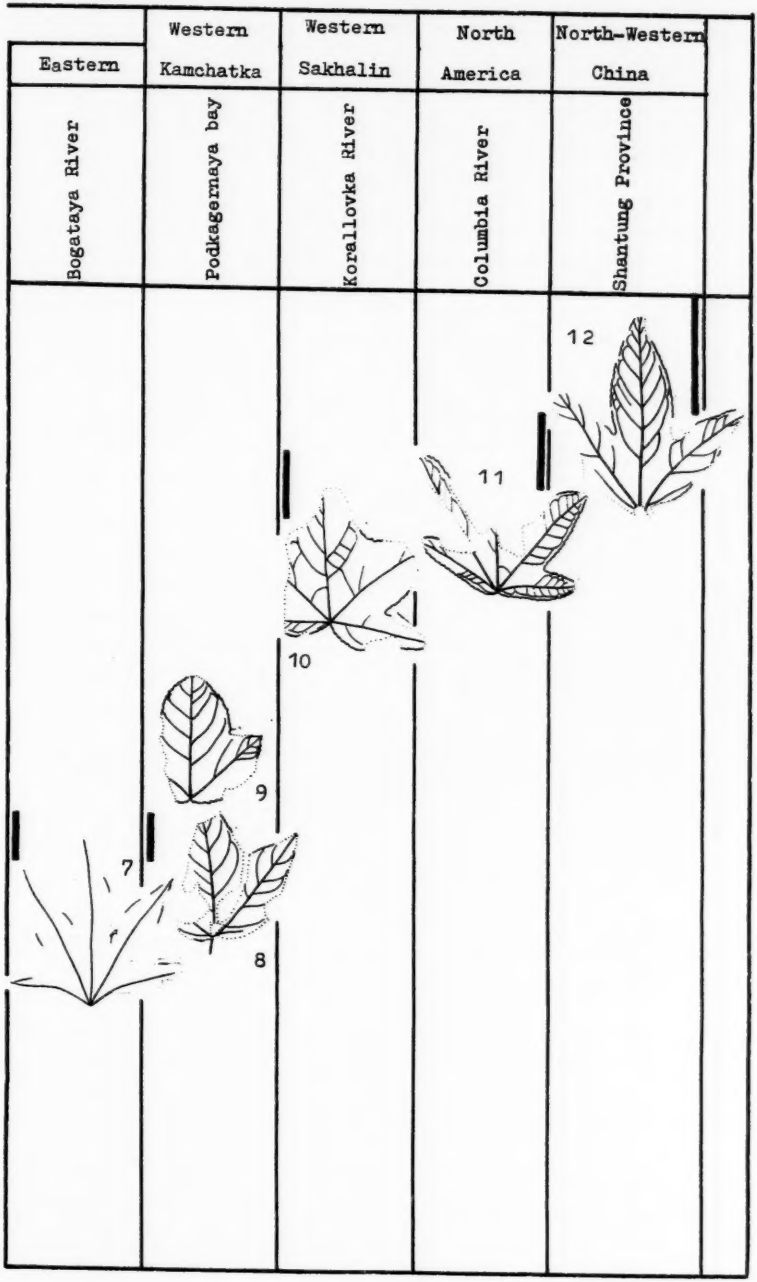
To the south, *Liquidambar* pollen occurred in Kamchatka (Snatolskaya Formation, Middle Eocene, and Cape Tons Formation, Upper Eocene) and Sakhalin (Krasnopol'yevskaya Formation, Middle Eocene, and Takaradaiskaya Formation, Middle-Upper Eocene) [9].

The largest amount (12%) of *Liquidambar* pollen is in the Eocene coal measures of Lower Bikinskaya Depression in northern Primor'ye [22].

Note: On Figure 2, see pp. 154-155.

Fig. 2. *Liquidambar miosinica* Hu et Chaney. 1 - Coll. 3736, No. 3736/6A-2, ×0.5; 2 - Coll. 4252, No. 29/75-3, ×0.5; 3 - Coll. 4252, No. 15H/74-1, ×0.5; 4 - Coll. 4253, No. 1/84-22a, ×0.5; 5 - Coll. 4448, No. 6/90-1, ×0.5; 6 - Coll. 4448, No. 3/90-227a, ×0.5; 7 - *Liquidambar pachyphylla* Knowlton, Coll. 4129, No. 4/84-209, ×0.25; 8-10 - *Liquidambar miosinica* Hu et Chaney: 8 - Coll. 3862a, No. 1b/16-79, ×0.5; 9 - Coll. 3862a, No. 4/85-4, ×0.5; 10 - Coll. 3782, No. 2b/70-1, ×0.5; 11 - *Liquidambar pachyphylla* Knowlton, No. 8534, lectotype, ×0.5; 12 - *Liquidambar miosinica* Hu et Chaney, No. 205, holotype, ×0.3.

Age
Western Kamchatka
Sakhalin
Western
Chemurnaut bay
Krasnoyarka River
Naiba River
Kama, Snezhinka, Aralskaya Rivers
Paleocene
Lower
Danian
Zel.
Upper
Thanet
Eocene
Lower
Ypresian
Middle
Lutetian
Barton
Upper
Priab.
Oligocene
Lower
Rupelian
Upper
Chattian
Miocene
Aquit.
Lower
Burdigal.
Lang.
Middle
Serrav
Upper
Tortonian
Mes
1
2
3
4
5
6


Eastern
Western Kamchatka
Western Sakhalin
North America
North-Western China
Bogataya River
Podkagernaya bay
Korallovka River
Columbia River
Shantung Province
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8
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12

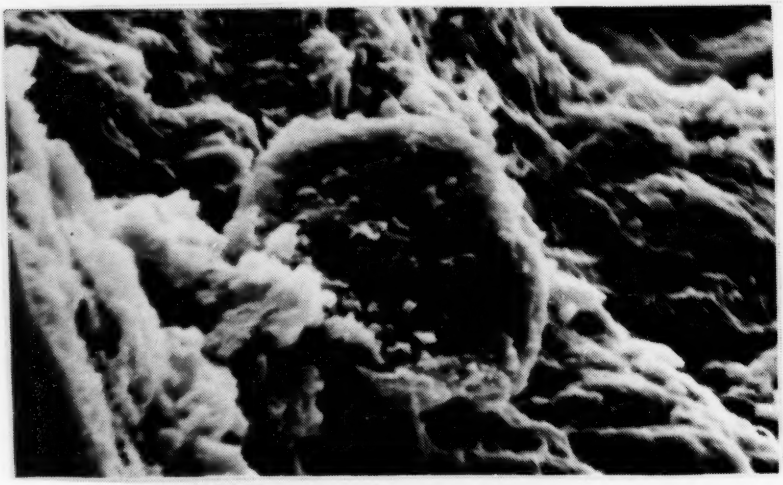

Fig. 3. Pollen grain on leaf impression of *L. pachphylla* Knowlton, SEM, ×3000.

The Oligocene pollen assemblages show a sharp decrease of *Liquidambar*. Some of the supposed Oligocene records [7] might actually came from Eocene deposits. Occasional grains have been reported from the Amaninskaya and the lower part of Utkholokskaya formations in western Kamchatka [9].

A brief recovery in the Miocene is evidenced by the pollen records from the northern coast of Chukotka [4], the northern coast of the Okhotsk Sea, Sakhalin [14], and Primor'ye [6].

Historical Sketch

Leaves of *Liquidambar* first appeared in the terminal Paleocene/Early Eocene in Kamchatka. They are absent in the Middle Eocene floras, but rather common in the Late Eocene, which is their last appearance in this area.

Liquidambar was widely distributed in the Middle to Late Eocene of Sakhalin. It is absent in the Oligocene and Early Miocene floras of this area. Its transient recurrence is associated with the Middle Miocene climatic optimum, perhaps by migration from a more southerly location in Japan, where this genus had reached its optimal development.

Subsequently *Liquidambar* history is that of drastic reduction of its ranges. Critical to its survival in northeastern Asia have been two cooling events: at the Eocene-Oligocene boundary, and in the Late Miocene. A distinctive feature of the genus is that it never achieved great taxonomic diversity. In this respect *Liquidambar* resembles *Nyssa* L., another widespread genus represented by a limited member of species.

Acknowledgments. The fossils were kindly provided by Dr. L. I. Fotyanova. I am also grateful to Prof. V. A. Krassilov for his constructive advice.

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CELL ULTRASTRUCTURE IN THE LEAF OF MIOCENE *Eucommia* WITH PRESERVED GUTTA-PERCHA THREADS (NORTHERN KAZAKHSTAN)

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Abstract. Leaves of Lower Miocene *Eucommia palaeoulmoides* Baik. from northern Kazakhstan contain gutta percha that has remained elastic for 25 mln years. Identification was based on tooth structure, characteristic venation, and the presence of gutta percha [8-12]. All the leaf tissues on cross sections — upper and lower epidermis, mesophyll (palisade and spongy parenchyma), and vascular bundles — are seen under the light microscope (LM). Virtually all cell organelles and their internal structure are visible on ultrathin sections (using TEM): chloroplasts with thylakoid system, mitochondria with cristae, cisternae of endoplasmic reticulum, nuclei and ribosomes. Cells of the epidermis and the mesophyll retained chloroplasts. The latter have a well-developed thylakoid system — granae and intergranal thylakoids are seen.

Листья *Eucommia palaeoulmoides* Baik из нижнего миоцена Северного Казахстана содержат гуттаперчевые нити, сохранившие эластичность в течение 25 млн. лет. На срезах различимы эпидермис, палисадная и губчатая ткани мезофилла, проводящие пучки. С помощью трансмиссионной электронной микроскопии Ёзучены хлоропласты, митохондрии, эндоплазматическая сеть, ядра и рибосомы.

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Introduction

In 1963 a geological survey was conducted in the northwest Turgay Lowland on the right bank of the upper reaches of the Tobol River [1]. The Cenozoic deposits were 198.5 m thick in borehole No. 138 at the bottom of drained Krugloe Lake. Their stratigraphic position was determined from the paleofloristic assemblage found in the lower part of the deposits (78-198.5 m deep), which were first dated as Late Oligocene on the basis of leaves, spores, and pollen collected at this depth [1]. Later, the comparison of floras from Krugloe Lake with a number of standard paleofloras (Oligocene-Early Miocene) from northern Ustyurt and northern Cis-Aralia produced a more precise age of the interval 102-137 m, and it was assigned to the Lower

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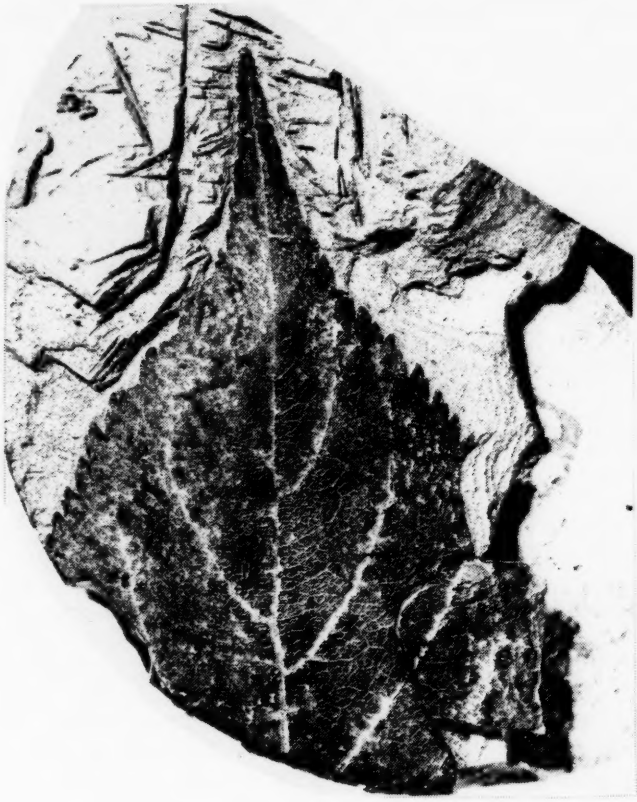

Fig. 1. Leaf compression of *Eucommia palaeoulmoides*, ×2.

Miocene, namely, to the Aquitanian [8, 11, 12]. Numerous compressions, or phytoleima, of dicotyledonous leaves and needle-bearing shoots of conifers were found in layers of diatomaceous clays (102-137 m interval): *Sequoia abietina* (Brongn.) E. Knobloch, *Taxodium dubium* (Sternb.) Heer, *Metasequoia disticha* (Heer) Miki, *Eucommia palaeoulmoides* Baik., *Pterocarya paradisiaca* (Ung.) Iljinskaja, *Ulmus carpinoides* Goepp., *Zelkova zelkovifolia* (Ung.) Bovek et Kotlaba, *Acer palaeosaccharinum* Stur, *A. aegopodifolium* Baik. ex Iljinskaja.

The excellent preservation of the four compressions assigned to *Eucommia* was quite surprising, and the geologists who collected them (V. A. Bronevoy, N. N. Bryzzheva, V. I. Baranov) and the paleobotanist (S. G. Zhilin) who made the plant identification were all equally amazed by this phenomenon. When sorting the collection, it was noted that four plates of clay (which had been split during collection) did not fall apart — they were kept together by elastic threads running from the compressions. The first supposition that it was gutta percha, and *Eucommia*, was soon confirmed. Identification was made by comparison with leaves of the modern species, *E. ulmoides* Oliv. (the extinct species, *E. palaeoulmoides* Baik., had not been yet established) — their venation and characteristic "double" teeth (like a smaller tooth mounted on a larger one)

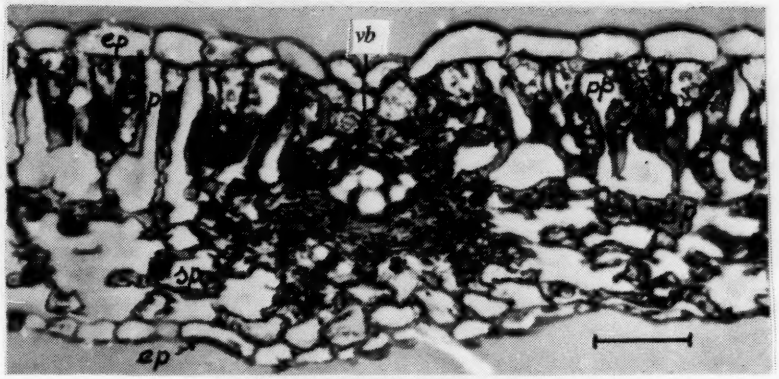

Fig. 2. Cross section of leaf (LM), scale bar = 5 μm. Abbreviations [in this and the following figures]: *c* - cuticle, *cg* - container of gutta percha, *ch* - chloroplast, *cw* - cell wall, *ec* - external cell wall, *ep* - epidermis, *er* - endoplasmic reticulum, *g* - granae, *is* - intercellular space, *it* - intergranal thylakoid, *lb* - lipidlike body, *mr* - microbody, *ms* - membranous structure, *mt* - mitochondrion, *mu* - mucilage-like body, *n* - nucleus, *og* - osmophilic granules, *p* - plastid, *pc* - primary cell wall, *pg* - perforated round body, *pl* - plastoglobule, *pp* - palisade parenchyma, *r* - ribosome, *sg* - starch granule, *sp* - spongy parenchyma, *st* - second thickening, *t* - tracheal element, *v* - vacuole, *vb* - vascular bundle, *zl* - zone with lines.

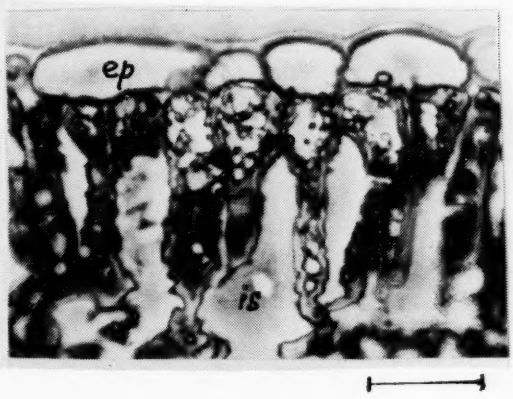

Fig. 3. Cells of upper epidermis and palisade parenchyma (LM), scale bar = 50 μm.

were very similar to our leaf compression. The presence of gutta percha appeared then as an accompanying and not a major feature.

It was particularly amazing that the threads of gutta-percha had remained elastic during such a long period (about 25 mln years) in the earth and during their storage for several years in a cardboard box. This was reported in several publications [8-12].

Good preservation of such a delicate structure as gutta-percha threads indicated that other details of its inner structure could be also retained in leaves of *E. palaeoulmoides*. The present work is based on the study of a small leaf fragment of *E. palaeoulmoides*, using light and transmission electron microscopes to determine the extent of preservation of tissues, cellular structures, and their components.

Materials and Methods

We took a small part of the compression (No. 2a, of No. 2 of Coll. 1018, Dept. of Paleobotany, Komarov Botanical Institute; fig. 1) for the study. The fragment of leaf compression was immersed in a fixing solution of 2% phosphate-buffered glutaraldehyde at PH 6.4 for 3-4 days at 0-+5 C°, washed with 0.1 M phosphate buffer, fixed for 14-16 hrs with buffered 1% OsO_4, dehydrated in acetone, embedded and polymerized in an Epon-Araldite mixture. All processes were at room temperature. Semithin (μm) and ultrathin sections were cut with a Reichert-Yung Ultracut microtome. Semithin sections mounted on slides were stained for histochemical identification in 5M KOH and Sudan III for lipids, and in phenol and oil of cloves for silicon [4]. The ultrathin sections were mounted on "Formvar"-coated copper grids and stained with lead citrate (5-10 min). The sections were examined with LMS NU-2, Ergaval with APL 0.9e, and TEM BS-500 (Tesla).

Results

A small fragment of leaf compression of *E. palaeoulmoides* was used to study cross sections with the LM. Cells of well-preserved upper and lower epidermis and mesophyll, as well as vascular bundles, are seen on slides (figs. 2, 3). Cells of the upper epidermis are quite large, about double the size of those in the lower epidermis, and appeared swollen. Cavities of irregular oval outline are visible on some cells of the upper epidermis, and are assumed to be mineral bodies. Pores are seen on the external wall of these cells. Similar cells are in groups of 3 or 4 above vascular bundles. On thin sections treated with phenol and placed in oil of cloves, the upper epidermis cells (walls and cavities) and cell walls of the whole set of vascular bundle became a pink-greenish color. Cell walls of palisade and spongy parenchyma were not stained and were not seen on sections. It is assumed that cell walls and epidermal cells contain silicon. Cells of the lower epidermis are somewhat contrasting to those of the upper epidermis. Stomata are found in the lower epidermis.

Palisade tissue consists of one row of cells that extend across the leaf section. LM reveals vacuoles with inclusions. Cells of spongy parenchyma are compressed, and vacuoles are not visible. Intracellular spaces are clearly distinct (figs. 3, 4*a*). Very large vascular bundles are on the boundary between the palisade and spongy parenchyma (fig. 2).

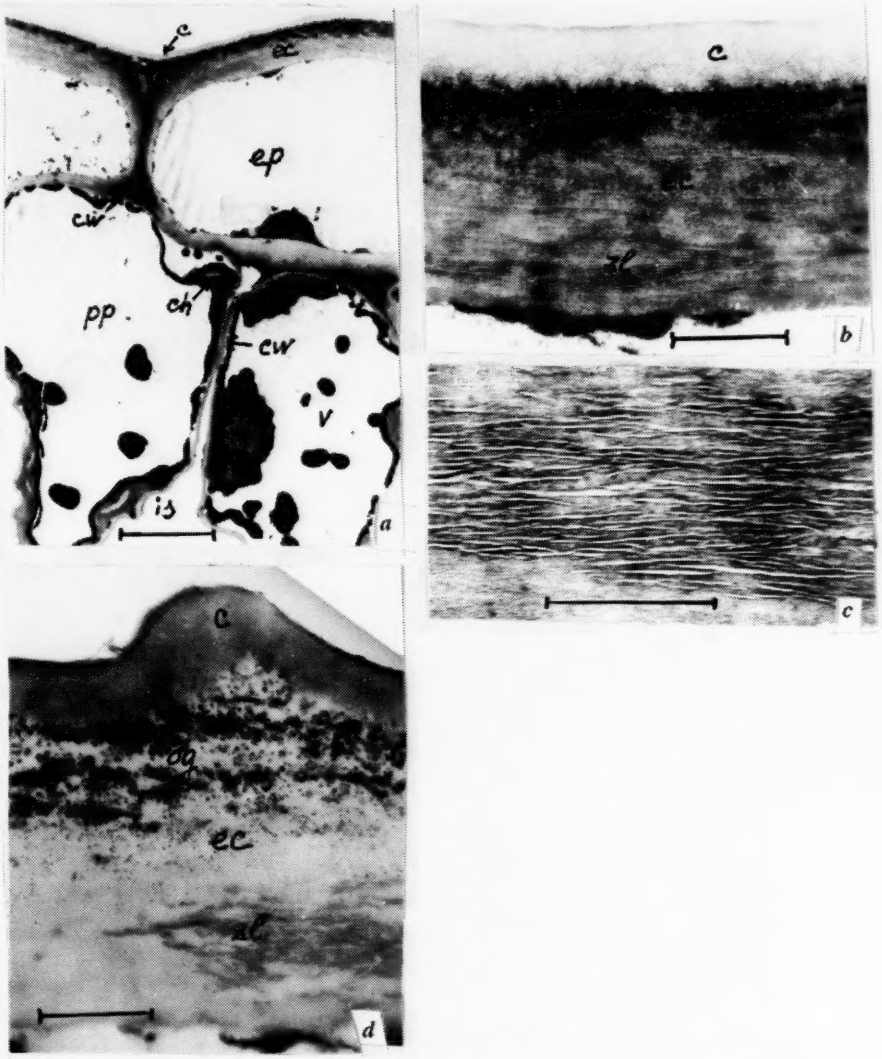

Fig. 4. General view and fragments of epidermis (TEM): *a* - epidermis and mesophyll, scale bar = 10 μm; *b* - cuticle and cell wall, scale bar = 1 μm; *c* - zone of cell wall with lines, scale bar = 0.5 μm; *d* - unstained cuticle, scale bar = 0.5 μm.

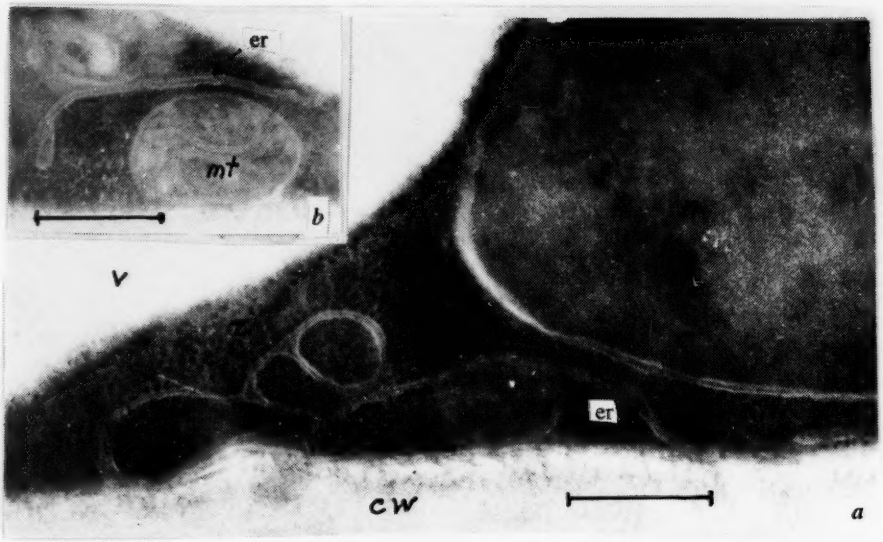

Fig. 5. Fragments of epidermal cells (TEM): *a* - nucleus and ribosomes, scale bar = 0.3 μm; *b* - mitochondrion and endoplasmic reticulum, scale bar = 0.3 μm.

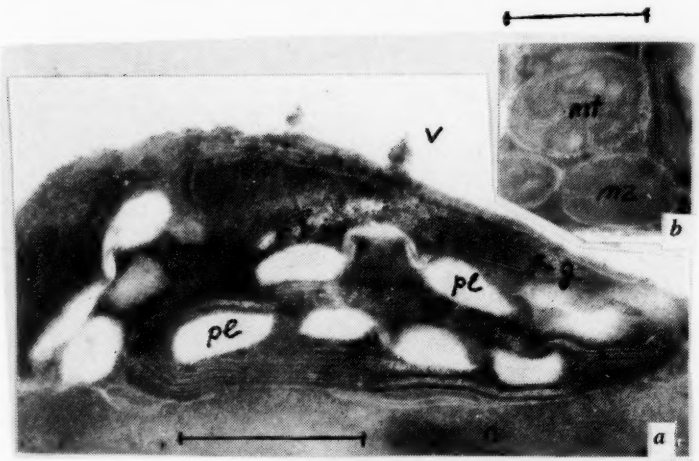

Fig. 6. Organelles of epidermis (TEM): *a* - chloroplast, scale bar = 0.5 μm; *b* - mitochondrion and microbody, scale bar = 0.3 μm.

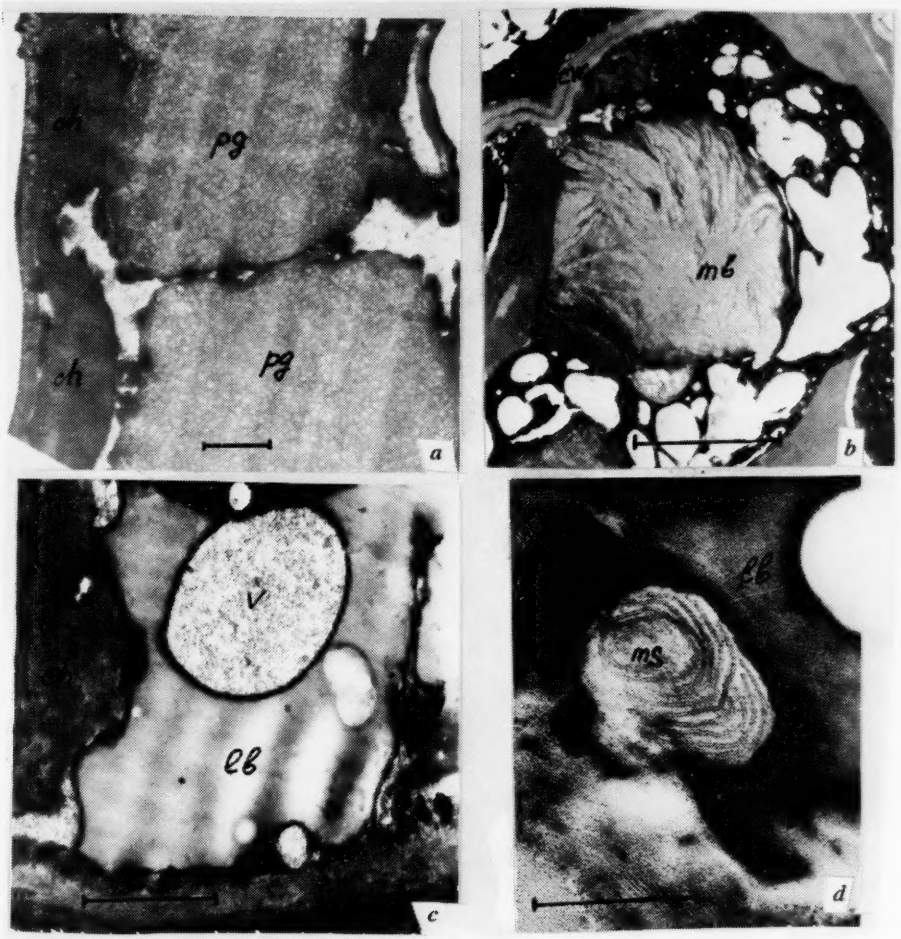

Fig. 7. Fragments of mesophyll cells (TEM): *a* - part of cell with perforated round bodies, scale bar = 1 μm; *b* - mucilage-like body, scale bar = 3 μm; *c* - lipidlike body, scale bar = 1 μm; *d* - membranous structure, scale bar = 0.3 μm.

Many cell components with well-preserved ultrastructure are recognizable on ultrathin sections. Outer cell walls of the upper epidermis are covered with a relatively thin cuticle with dendrites (fig. 4*a*, *b*). Directly under the cuticle is a layer of spheric osmophilic granules (fig. 4*b*, *d*). In the inner layer of external cell walls a "zone with lines" that contains several layers of light bands of varying length (fig. 4*b*, *c*) can be seen. This zone, clearly visible on sections not stained with lead citrate, is similar in density to the cuticle (fig. 4*d*).

Dendrites are not seen on unstained sections in the cuticle. However, the lower layer of spheric granules contrasts sufficiently and is clearly visible.

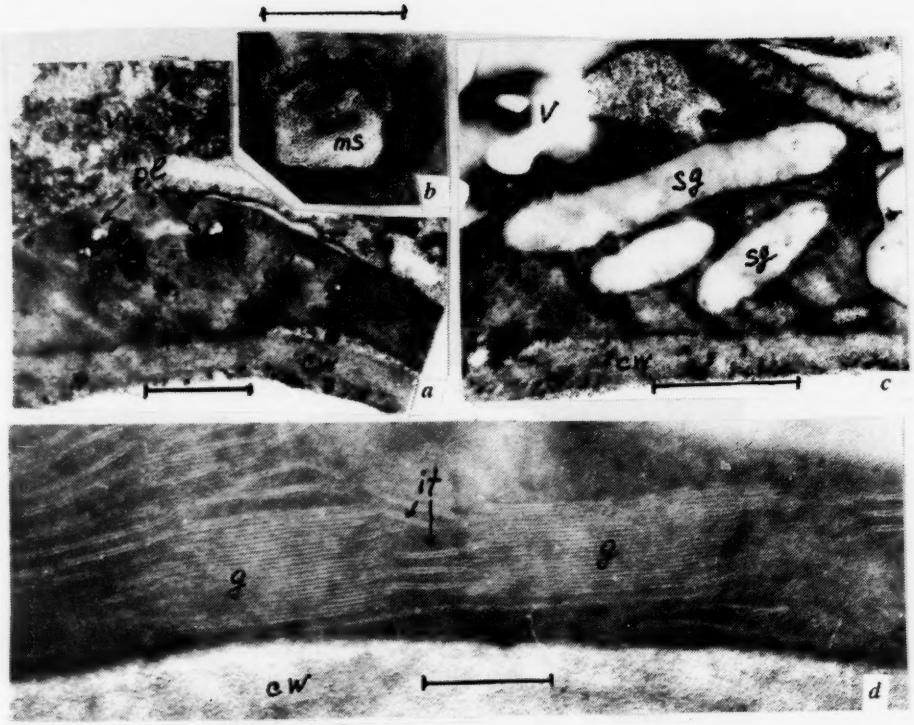

Fig. 8. Plastids of mesophyll cells (TEM): *a* - chloroplast with osmophilic plastoglobules, scale bar = 1 μm; *b* - plastoglobule with concentric membranes, scale bar = 0.25 μm; *c* - chloroplast with starch granules (grains), scale bar = 1 μm; *d* - the thylakoid system, scale bar = 0.2 μm.

On thin sections, external cell walls were stained yellow, due to alkali. The cuticle and thin inner layer of the external cell wall were stained intensive pink with Sudan III. In some cells, parts of the inner tangential cell walls of the epidermis also became pink.

These results suggest that the external cell walls of the sample contain cutin and suberin that are concentrated in the "zone with lines" and the cuticle. In the upper and lower epidermal cells there are elongated nuclei with a double membrane and pores (fig. 5*a*). Mitochondria (fig. 5*b*) and occasionally microbodies (fig. 6*b*) are seen around the nuclei. Near the nuclei are separate cisternae of endoplasmic reticulum (ER), ribosomes (fig. 5*a*, *b*), and small vacuoles (vesicles) with light lipidlike globules surrounded by 2-3 layers of membrane pairs. Chloroplasts with athylakoid system are found in epidermal cells (granae and intergranal thylakoids are visible) (fig. 6*a*). Light plastoglobules and cavities are in plastids of the epidermis (fig. 6). It can be seen in some cases how the substance of plastoglobules is discharged into the vacuole.

Vacuoles of many cells of the palisade parenchyma have "perforated"-round bodies (fig. 7*a*), two-thirds of which are found in some mesophyll cells. Sometimes, in vacuoles of palisade

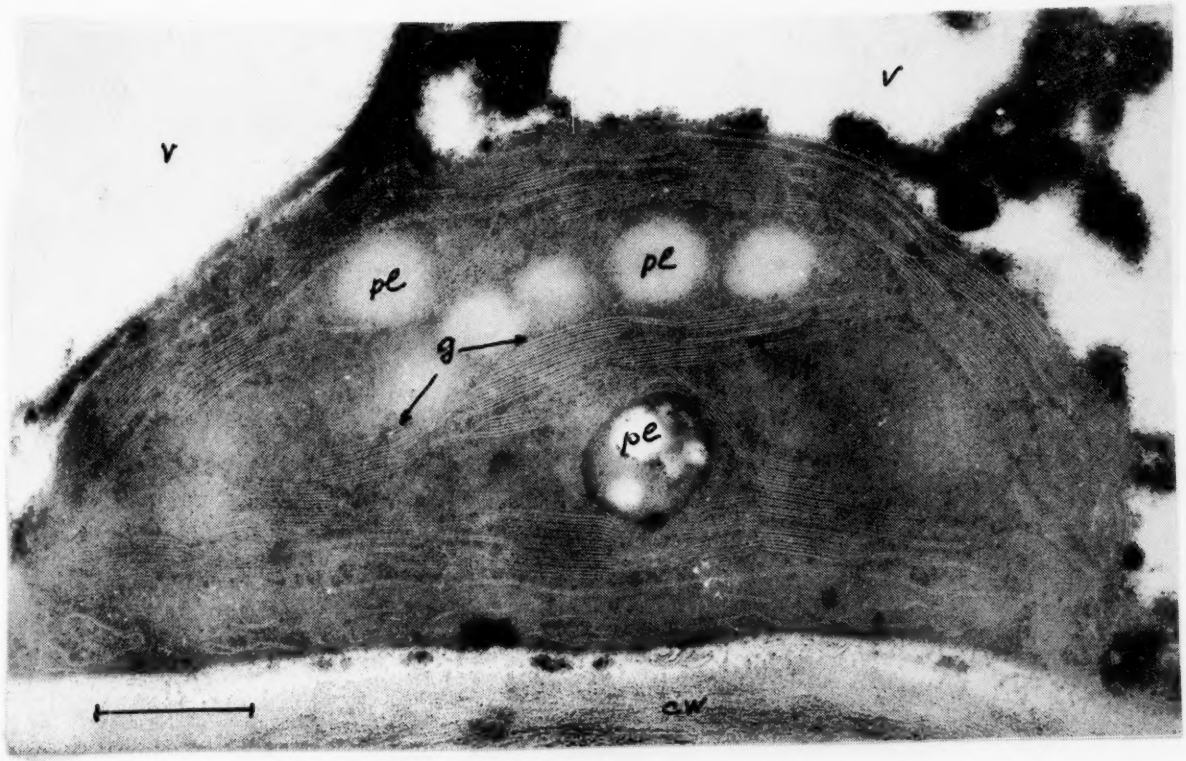

Fig. 9. Chloroplast (TEM), scale bar = 0.3 μm.

parenchyma cells there are large globules (presumably consisting of mucilage) among the osmophilic substance (fig. 7*b*).

Mesophyll cells nearer the vascular bundle have lipidlike inclusions with osmophilic rims in their vacuoles (fig. 7*c*). Near these inclusions there are curved bilayer membranes (fig. 7*d*), which probably are lipid derivatives.

Distinct chloroplasts are in the outlying area of the mesophyll cells along cell walls (figs. 4*a*; 7*a, c*; 8*a, b, c*). They contain light osmophilic plastoglobules (figs. 8*a*; 9) and elongated starch grains (fig. 8*c*). In some cases concentric membranes are in osmophilic plastoglobules (fig. 8*b*). The thylakoid system of chloroplasts is clearly discernible, with granae and intergranal thylakoids (figs. 8*d*; 9). Granae frequently consist of 20 and more thylakoids.

It should be noted that all membranes of chloroplasts, mitochondria, nuclei and endoplasmic reticulum have "inverse (negative) contrast." This gives an impression that the fossil material retained not membranes themselves, but shadows or places where membranes had been. On the other hand, the membranes not involved in organelle construction are very well preserved, e.g., membranes near lipidlike sediments (figs. 7*d*; 8*b*). Similar membranes are frequently observed near chloroplasts adjacent to the cell wall and also in periplasmic space of epidermal and mesophilic cells.

Xylem and phloem parts are discernible in vascular bundles (figs. 2; 10*a*). The xylem consists of two types of tracheal elements, primarily differing in size. Large tracheal elements have secondary thickenings which are occasionally disrupted and secondary thickenings which are occasionally disrupted and form pores (fig. 10*b*). The primary cell walls in pores are not reduced (fig. 10*b*). The diameter of tracheal elements of the second type is approximately 1/2 that of the first type. Secondary thickenings usually take up 1/3 of the vessel cross section. Most of the vessel has perforations whose primary wall is reduced to fibrils. Among the compressed cells of the phloem part (near the boundary with spongy parenchyma) there are small round or elongated cells filled with homogenous thick substances with no signs of organelles (fig. 10*c*); these are presumably cross sections of gutta percha "containers." About 6 or 7 such "containers" can be found in large vascular bundles (fig. 10*a*). Clusters of mitochondria are seen in some elongated and compressed cells of the phloem part.

Conclusions

Although only a small fragment of the compression (split during preparation) of the principal specimen was investigated, we can state that the preservation of the plant remains from borehole No. 138 is really amazing. Apart from the elasticity of the gutta percha threads (noted in 1963 during collection and preparation [8-12] of all four specimens), the present study has showed that the leaf compression retained virtually all of the structural cell components. Although no apparent degradation of cells and organelles was observed in the samples, we should recall that the fossil leaf structure was retained in the form of a peculiar shadow. The term "inverse (negative) contrast" has long been used for membranes that have undergone some changes (this happens both in fossil and herbarium material). We can suppose that "inverse contrast" indicates one of the stages of "replacement of organic substance with mineral," a well-known phenomenon in paleontology. The stage we are observing is entirely "organic," because one substance inherent in the plant is replaced by another organic substance. These structures

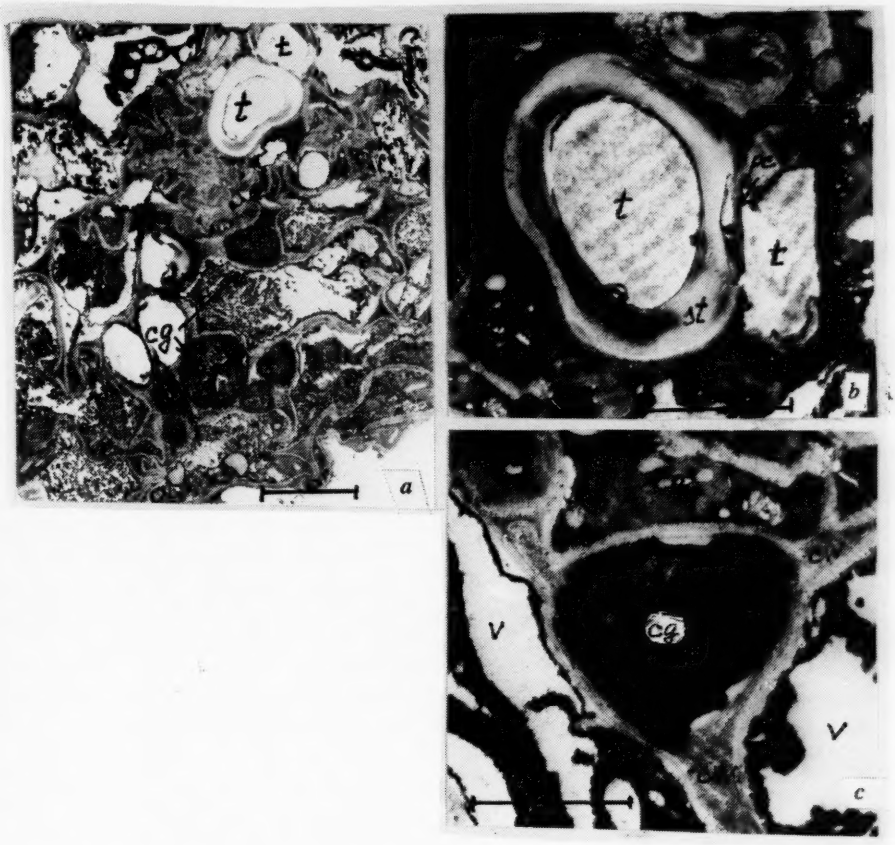

Fig. 10. Vascular bundle (TEM): *a* - general view, scale bar = 10 μm; *b* - tracheids, scale bar = 3 μm; *c* - container of gutta percha, scale bar = 2.5 μm.

were perhaps transformed after burial. The preservation of our compression is much better than that of Miocene fossils of *Clarkia* in Succor Creek [3]. For example, no endoplasmic reticulum is found, and no ribosomes are reported in American samples by Niklas [3]. Special attention was paid to the preservation state of nuclei because they are the elements in fossils that are primarily subjected to degradation [3]. The sample of *E. palaeoulmoides* has nuclei, ribosomes and ER. Of particular interest are membranous structures of "normal contrast" from cells of the epidermis and mesophyll (figs. 7*d*; 8*b*).

Membranous structures are frequently in contact with lipid bodies, and seem to contain considerable quantities of lipids, which are major membrane components [5]. The "inverse contrast" of membranes, organelles (nuclei, microbodies, mitochondria with cristae and chloroplasts with thylakoid system), and "normal (positive) appearance" of the membranous

structures that are not involved in organelle formation seem to be an indication of a much better preservation of lipids than of proteins in fossils.

The earlier supposition about the rapid sedimentation during the formation of Krugloe Lake 25 mln years ago [1] can only partly explain the excellent preservation of plant remains from the core sample of borehole No. 138. It should be noted that only the plants were well preserved, while several small fish fragments could not be identified at the generic level due to their poor preservation (pers. comm., 1964, paleoichthyologist P. G. Danilchenko).

During the SEM study of the fossil gutta percha threads in 1978, Zhilin found that clays were abundant with diatoms. Therefore, it was natural to suppose rapid sedimentation as the result of intensive proliferation of diatom flora; but preservation of plants even in pure diatomite is not necessarily a guarantee of their good preservation. Favorable conditions for the preservation of fossil plants could be due to a combination of various factors acting simultaneously at the same place. The major condition of good preservation of phytofossils is their long existence (thousands and millions of years) in an oxygen-free environment.

The next most important factor is their rapid burial (as in Krugloe Lake). In our case, an essential factor was the formation of a peculiar "sarcophagus" of carboniferous red-brown sandstones (due to fractures and rapid subsidence of a small area not exceeding 1 km in diameter). The "sarcophagus roof" is formed by a thick lignite layer that originated during the marshy developmental stage of Krugloe Lake (Late Miocene-Pliocene). Finally, is the conserving effect of silicon, which is a component of sedimentation material (diatom shells). It should be noted that cell walls and vacuoles of extant [6] and fossil species of *Eucommia* contain silica. In addition to general proposals on the role played by silicon in strengthening the cell walls, there are works dealing particularly with its role in retarding the development of fungal infections [2].

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PALEOBOTANICAL DATA ON THE GEOLOGICAL AGE OF THE GREATER CAUCASUS

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Abstract: New finds of Oligocene and Miocene terrestrial plants from the shallow marine deposits along the axial zone of the Greater Caucasus Range provide chronological evidence of the first land in this area.

Новые находки растений в хадумских и чокракских отложениях и анализ прежних данных позволяют датировать последовательные события в развитии массива суши на месте Большого Кавказского хребта.

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For many years geologists and paleogeographers have been interested in the Cenozoic history of insular land in the Greater Caucasus, or "Yaphetida." All the successive developmental stages of this mountain building seemed clear in the first half of this century. Using Palibin's results [15] and in accord with Andrussov and other geologists, E. V. Wulf [21] wrote: "The Greater Caucasus emerged as a land stretched along the main ridge at the end of the Cretaceous. Its size increased or decreased with transgressions and regressions during the first half of the Tertiary. . . . By the end of the Miocene the strait separating the Greater Caucasus from Asia Minor (which included the Lesser Caucasus) had disappeared, and the Greater Caucasus became connected with the latter."

After fifty years, we can state with more confidence that the first connection of the Greater and Lesser Caucasus land masses occurred in the beginning of the Late Sarmatian. From this time on the Greater Caucasus became an active mountain area, while its Pontian and Caspian parts became more and more floristically differentiated.

The preceding Cenozoic history of the Greater Caucasus, discussed below, appears less straightforward, but rather complex, as demonstrated by the UNESCO/IGU Geological correlation Programme Projects Nos. 174 and 326. B. A. Onishchenko [14] suggested that the Greater Caucasus was uplifted above sea level in the region of active erosion at the Eocene boundary. This was evidenced by the regional unconformity between the Lower Oligocene Maykop deposits and the underlying pelagic Upper Eocene Belaya Glina Formation.

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According to another extreme opinion, the Greater Caucasus was the area of inflow of marine sediments until the Middle Sarmatian and could not have been the source of detritus. Erosion of the underlying deposits and olistostromes indicate submarine conditions.

The facial analyses has shown that almost everywhere the plant-bearing beds alternate with those containing marine mollusks, and occur along the ancient sea coasts. For example, the majority of the Paleogene flora localities are associated with the margins of the ancient Georgian block as well as with the rises of the Lesser Caucasus and Talysh, while the Upper Miocene and Pliocene localities are confined to the margins of the Kura and Rioni basins, as well as the depressions of the Georgian block. The localities are rarely associated with volcanic zones and continental molasses in small intermountain depressions.

The author has found the oldest Paleogene terrestrial flora in the Kuban reference section near Cherkessk. In the middle part of the Kuma Horizon is a layer saturated with leaf-fragments, and with rare complete leaves of *Myrica* and Fagaceae. Abundant plant debris in the Kuma siltstones, together with leaf impressions, suggests a nearby source. A pollen assemblage from the plant remains, made by N. I. Zaporojets, indirectly confirms this suggestion. Together with saccate conifer pollen that is easily transportable, at least 50 taxa of angiosperm pollen were recorded (Hamamelidaceae, Ulmaceae, *Rhus*, Sapindaceae, Araliaceae, *Tilia*, Moraceae, etc.).

The absence of shallow-water and continental deposits in the Kuma Formation of the cored Stavropol Arch suggests the presence of a small island to the south, in the axis area of the Greater Caucasus during the Middle Eocene. It was partly caused by the Paleogene submarine Adygeen uplift.

The homogeneous pelagic sediments of the Upper Eocene Belaya Glina Formation are very thick and also are the richest microplanktonic assemblages from both the northern monocline and the fault zone of the southern slope of the ridge. These support the contention that the Greater Caucasus was submerged in the Late Eocene. The more shallow-water deposits from the southern Kakhetia fold zone of the Greater Caucasus southern slope in comparison with the northern (Chiatura) zone [7, p. 10] testify to the influence on sedimentary processes of the Georgian block to the south.

Reliable evidence of the existence of insular land within the Greater Caucasus in the western and eastern submerged areas of this large morphostructure is now available for the Early Oligocene.

J. Felix [4] studied the collection of fossil woods made in the Sumgait River basin at the end of the century by Sjorgen's expedition, organized by Nobels for research in the Baku oil region.

In the 1930s I. V. Palibin collected plants from Verkhniy Perekischkjul on the Sumgait River, and found some new localities on the Apsheron Peninsula near the Esry-Chale salt marsh. I. A. Shilkina [18, 19], who revised some of these plant identifications, considered *Plataninium porosum* J. Felix, *Laurinoxylon aromaticum* J. Felix, *L. maikopiae* (Jarm.) Shilok., and *Quercinium unibe* the most reliably identified from both localities. Taxodiaceae, Pinaceae, Ebenaceae and Theaceae woods were also found there. Their autochthonous origin is undoubted. Some fragments of roots with diameters up to 0.5 m are covered with sand. Palibin described leaves of *Pinus praepithynsa*, *P. maikopiae*, and *Cinnamomun* from the Lower Oligocene of the Sumgait-

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PLATE I

Apsheronian district. Algae, crabs, fishes, and cetacean bones were found in Verkhniy Perekischkjul, which confirm littoral sedimentation. The insular land area was more than 100^2 km. It was a submarine cordillera partly emerged above sea level. North of the insular land Lower Oligocene deposits are 2000-3000 meters thick and they contain thick olistostromes [9, 17]. The second insular land was located on the western dip of the Greater Caucasus in Tsitse, Pshekha, Pshish, and Belaya river basins, and extended for more than one hundred kilometers. Fossil plants collected from several localities were all found in the lower part of the Khadum strata below ostracod beds.

Of considerable interest is the fossil wood from Pshekha Basin (Pshekhian tributaries—Tsitse and Kara Tsitse). V. G. Hayvoronsky [5, 6] described Taxodiaceae, *Juglans*, *Quercus uniradiatum* (J. Felix) Jarm., *Quercus* cf. *petraea* Liebl., *Castanopsis* sp., etc. Palibin [15] found red and brown algae from the Khadum near Sevastopol Station as well as leaves of *Carpinus betuloides* Ung., *Quercus lonchites* Ung., *Laurus princeps* Heer, *Cinnamomum rossmaeslery* Heer. A. F. Bannikov collected a few fossil plants from the base of the Khadum strata on Belaya River near Abadzekhskaya Station, from which I identified *Pinus* sp. (samara), *Taxodium dubium* (Sternb.) Heer, *Cryptomeria* sp., *Litsea* sp., *Cinnamomum cinnamomeum* (Rossm.) Hollick, *Dryophyllum furcinerve* (Rossm.) Schmal., Leguminosae gen. et sp. indet., *Apocynophyllum helveticum* Heer (Pl. I, fig. 2).

At the beginning of the Oligocene, the western Caucasus insular land was inhabited by Lauraceae and evergreen Fagaceae; these indicate the subtropical climate as the wood of the seashore zone is very similar to that of the western Paratethys. The Greater Caucasus was submerged again in the Late Oligocene until the end of the Early Miocene. Marine microplankton predominated in the clayey facies of the northern monocline. Macroscopic plants are absent from these shallow-water marine deposits. The sedimentation occurred in an anoxic deep-water basin. Submarine landslides were common in this basin. The Metkhi flora was found near Gori between Uplistsikhe beds of Aquitanian age and Sakaraulian strata of Burdigalian age [2]. This flora probably did not come from the Greater Caucasus but was derived from the Dzirula Massif. We have data on new insular lands along the Greater Caucasus axis zone only from the beginning of the Middle Miocene. Fossil plants were found in many places on the northern monocline, but in the western part only in Chechen, Dagestan and Azerbaijan between Grozny and the Apsheron Peninsula; they are from shallow-water deposits of consedimental folds indicating the ancient coastal line.

I have studied plants from the Lower Chokrakian horizon that were collected by V. N. Kholodov and Yu. O. Gavrilov [8] in the Chechen-Grozny Basin. They were found on the right bank of the Fortanga River on oligomiotic siliceous sandstones, near the top of the Mikhailovsky

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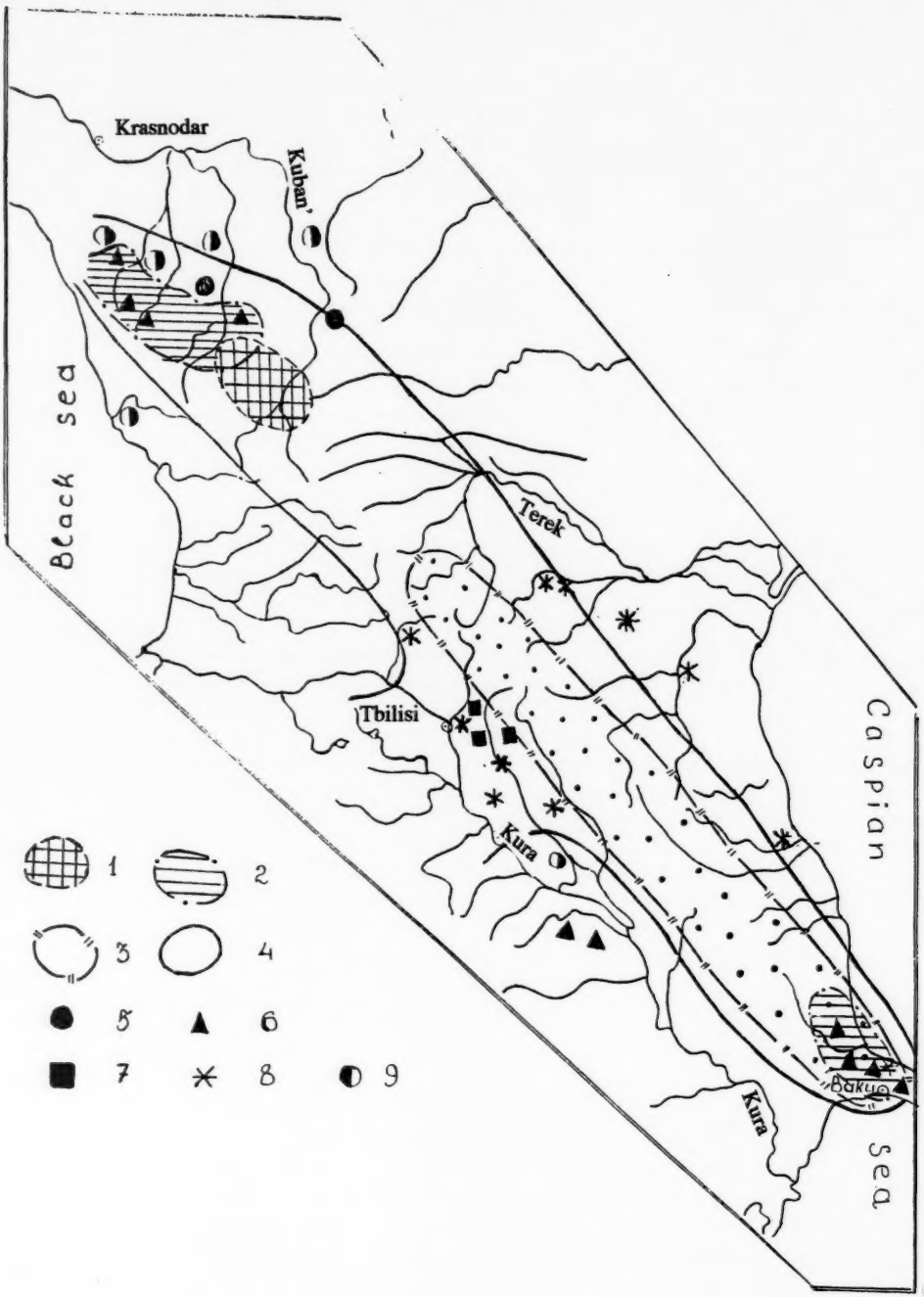
KEY TO PLATE I

Lower Oligocene plants from Khadum strata on Belaya River. Coll. No. 5003, Geological Institute, Russian Academy of Sciences, Moscow. 1 - *Myrica* sp., No. 3/5003, ×1.5; 2 - *Cinnamomun cinnamomeum* (Rossm.) Hollick, No. 5003, ×2; 3 - *Cryptomeria* sp., No.2/5003, ×1.5; 4 - *Litsea* sp., No. 6/5003, ×1.5; 5 - *Dryophyllum furcinerve* (Rossm.) Schmal., No. 1/5003, ×1.


Krasnodar
Kuban'
Black sea
Terek
Tbilisi
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Caspian
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sea
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horizon of the Chokrakian stage. Round or round-cylindrical tubers, 8-10 cm long and 2-3 cm in diameter (fig. 3), concentrated in the upper part of a silt layer, are traced more than 0.5 km. Usually they have a well preserved "neck" connected to the stem or to similar tubers below the surface of the ground. Their bases are broad-rounded, usually slightly blunt, and show numerous pointed holes from hairs. Sometimes the tubers are connected with each other by a thick short stem. The tuber "neck" turns vertically or penetrates the matrix. Usually the tubers have an outlet to the surface of the silt strata, which was hardground during the plant's life. These tubers may belong to different monocotyledons, e.g., Aponogetonales, Liliales, Zingiberales, Dioscoreales, etc.

The tuber-bearing strata appeared in the Early Chokrakian in relation to the rise of the Dattykh and Nazran anticlines, and the tuber horizon marked the ancient seashore facies. The plants might have grown in a stagnant lagoon. The evaporitic Chokrakian Dattykh Formation overlies the tuber strata. Palibin [15] has also recorded a flora from the Chokrakian of the northern Caucasus. The fossil plants were collected on the Terskiye and Sudzhensky ridges, in Dagestan, and Apsheron Peninsula. A stalk of *Zizyphoxylon* was found with Spireales in the latter district. *Staphylea* and riverside plants *Spirodela mironovii* Palib., *Salvinia sunskae* Palib., and *Phragmites oenengensis* Heer were collected near Groznyy (Sudzhensky Ridge). Palibin [15] found *Populus Mirabilis* v. *loveifolia* Heer, *Sapindus falciformis* Al. Br., *Cinnamomun scheucheri* Heer east of Groznyy, and *Myrica hakaefolia* Ung., *Laurus princeps* Heer, *Apeitopsis, Leuchothoe, Diospyros* in Rubas-Chai Valley, Terskiye district, Dagestan, in coarse terrigenous facies with *Spaniodontella*. T. N. Baykovskaya [1] described the palm *Sabal major* Ung. from Karaganian beds of the Sumgait basin, *Cystoseira, Cystophyllun* and *Sargassum* [10] were collected from the Karaganian near Maykop (western part of the Greater Caucasus). These finds supported the assumption that marine sedimentation persisted at least until the Sarmatian, and I cannot suggest the presence of a large insular land here at that time. The Greater Caucasus became mountainous only in the second part of the Sarmatian. Alluvial conglomerates with Cretaceous pebbles were found in the Terskiye Caspian Basin outlying the Greater Caucasus Ridge of that time, and the conclusion is that the Greater Caucasus was subjected to erosion. Rhythmic layered clinoforms of seashore pebbles overlap on the southern slope of the Greater Caucasus in Abkhaziya, Kakhetiya, Northern Cabystan [9, 17].

Lower and Middle Sarmatian floras are known from different localities in the Greater Caucasus periphery [3, 13, 15, 16, 20]. The Lower Sarmatian plants and marine mollusks occur together in the same strata, marking the ancient seashore. The Middle Sarmatian floras concentrate in delta and estuaries. The subsequent migration of the ancient seashore was related to the enlargement of this insular land from Early to Late Sarmatian. Essentially, paleogeographic restructuring of the Caucasus Region took place at the beginning of the Late Sarmatian. Two main land massifs—Greater and Lesser Caucasus—were isolated far apart, while the Dzirula massif, with adjacent islands, formed an archipelago system. During the Late Sarmatian an isthmus formed between the Greater and Lesser Caucasus ranges separating the Black and Caspian basins.

Fig. 1. Main localities of the Greater Caucasus and the insular land position: 1 - Middle Eocene; 2 - Early Oligocene; 3 - Middle Miocene; 4 - Late Miocene. Plant localities and their ages: 5 - Middle Eocene, 6 - Early Oligocene, 7 - Early Miocene, 8 - Middle Miocene, 9 - Late Miocene.

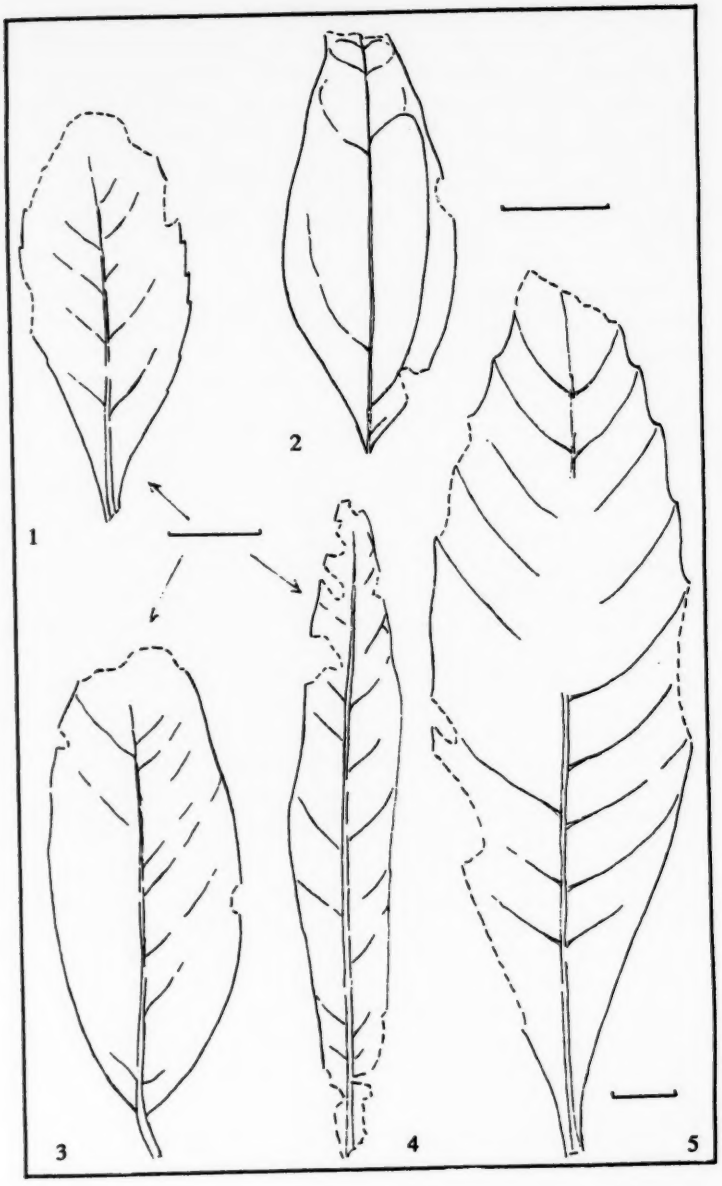
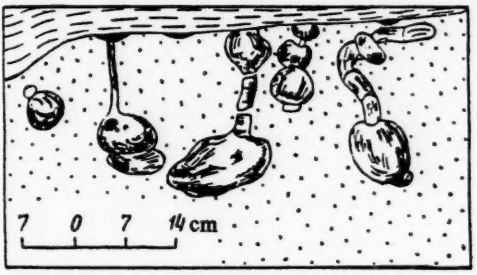
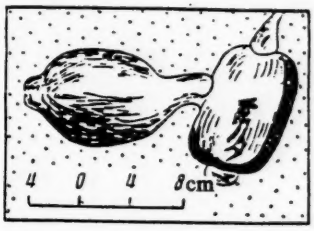


Fig. 2. Lower Oligocene plants from Khadum strata on Belaya River. 1 - *Myrica* sp., No. 3/5003, ×1.5; 2 - *Cinnamomum cinnamomeum* (Rossm.) Holl., No. 5003, × 2; 3 - Leguminosae gen. et sp. indet., No. 12/5003, ×1.5; 4 - *Litsea* sp., No. 6/5003, ×1.5; 5 - *Dryophyllum furcinerve* (Rossm.) Schmal., No. 1/5003, × 1.



a

c



b

Fig. 3. Tubers and their position in the Chokrakian of the Chechen-Groznyy Basin. *a* - Outcrops with tubers, right bank of Fortanga River; *b* - tubers in situ; *c* - typical tuber. Key: Dots - sands and silts; horizontal hatching - clays and argillites; black lenses - sideritic concretions at contact between sands and clays.

A main reason for the drier climate in the eastern Caucasus was the elimination of the strait between these basins at the end of the Sarmatian. Thus, the principal distinctions between West and East Transcaucasia developed. These local events were additional causes of the global cooling of the late Middle to early Upper Miocene.

The Lower and Middle Sarmatian floras of the Caucasus and Transcaucasia were subtropical, with more small-leaved plants in the eastern part. The Late Miocene Caucasian floras [3, 11] represented deciduous vegetation, part of them identical to Recent species. The main structure of the Greater Caucasus was formed only after the Late Sarmatian; its northern slope was involved in orogenic movements. The younger deposits — the Maeotian and Kimmerian — were absent or were incorporated in the proluvial facies with fragments and pebbles of the Central Caucasian rocks. Coastal deposits of the same age included Paleogene and Cretaceous pebbles from the Greater Caucasus along the southern margin of the western Kuban Depression.

The position of the Caucasian insular land was reconstructed on the basis of fossil plants and lithological analyses of the various stages in the Paleogene and Neogene. A small island existed in the western part of the Kuban Basin in Kuman time (latter half of the Middle Eocene). At the beginning of the Oligocene, two insular lands emerged on the western and eastern flanks of the main ridge. The larger western ridge persisted until the latter half of the Oligocene. In the beginning of the Middle Miocene, the eastern insular land appeared, and extended more than 500 km from Groznyy district to the Apsheron Peninsula. In the early half of the Sarmatian this island expanded, especially in the western area. The border of this land reached to the extant Black Sea. In the Late Sarmatian, the Greater Caucasus was transformed into a large montane system connected to the Lesser Caucasus by the Dzirula isthmus. The former island became a peninsular land.

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SHORT NOTES

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Paleontological Journal, 29(1A), 1995

Pseudotorellia FROM THE LOWER CRETACEOUS COAL-BEARING DEPOSITS OF EASTERN TRANSBAIKALIA

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Abstract. *Pseudotorellia kharanorica* n. sp. Bugdaeva is from Kharanor Suite of Chita Province, eastern Transbaikalia. *Pseudotorellia* seem to have been a dominant plant of the peat bog communities.

Новый вид *Pseudotorellia kharanorica* из харанорской свиты Читинской области отличается от других видов узкими заостренными килеватыми листьями, беспорядочно расположенными устьицами без папилл, прямыми или мелкоизвилистыми стенками эпидермальных клеток.

• • •

Several lower Albian coal mines in Chita Province, eastern Transbaikalia, contain a diverse fossil flora [1]. In the Kharanor mine, plant remains are from the minable coal as well as from the overlying shales and tuff. Macerated coal contains fragmented leaves of *Pseudotorellia* and shoots of the brachyphyllous conifer *Pagiophyllum*. Compressions of *Pseudotorellia* constitute up to 90-100% of the samples. Notably, *Pseudotorellia* shows frequent fungal damages which is absent in *Pagiophyllum*.

In the overlying shales, the needle-leaves of a conifer *Pityophyllum* typically are more common than *Pseudotorellia*, while *Pagiophyllum* is absent. Some plant beds contain monodominant assemblages with *Pityophyllum* or the bennettite *Nilssoniopteris*, while ginkgophytes are rare.

These observations indicate that *Pseudotorellia* was a dominant peat bog plant and a major producer of leaf coals. Other *Pseudotorellia* species are also from coal beds [3].

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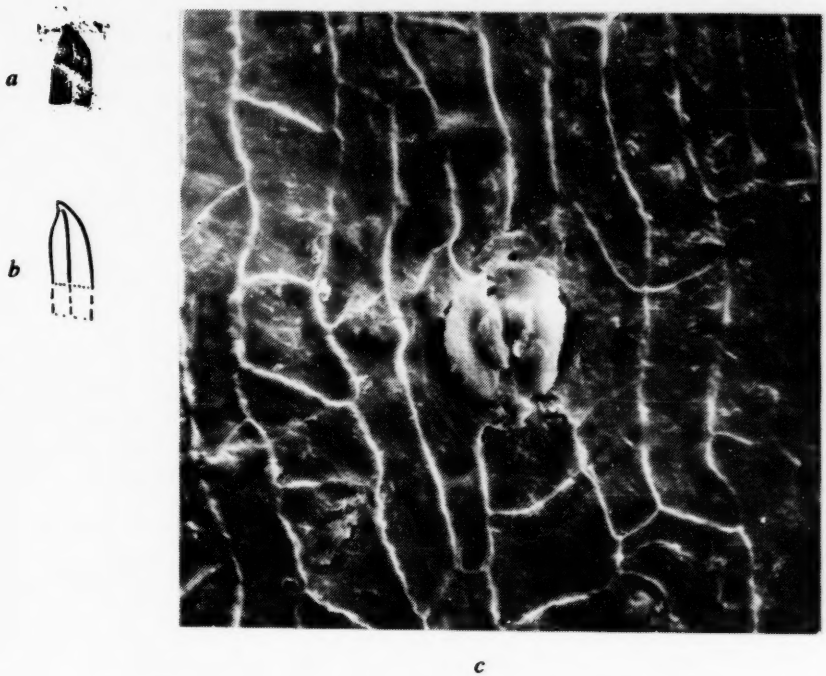

Fig. 1. *Pseudotorellia kharanorica*, sp. nov.: *a, b* - distal part of leaf, Holotype No. 313522/4-6766, ×1; *c* - stoma on lower cuticle, SEM, ×1000.

Pseudotorellia kharanorica Bugdaeva, sp. nov.

Fig. 1

Name. After the type locality, Kharanor.

Holotype. No. 313522/4-6766, deposited in Institute of Biology and Pedology (fig. 1); Kharanor mine, Chita Province, Transbaikalia.

Diagnosis. Leaves linear-oblanceolate, 2.4 mm wide, keeled, with mucronate apex. Venation inconspicuous. Upper cuticle showing elongate retanguloid, trapezoid, or irregular cells. Average dimensions of elongate cells 90-110 × 22-28 μm, of irregular cells 50-70 × 30-40 μm. Periclinal walls with more-or-less conspicuous median ridge. Anticlinal walls straight along margins, microsinuate in middle part of leaf. Lower cuticle showing stomata scattered all over leaf surface, not differentiated into definite stomatal bands. Stomata with five to six subsidiary cells, nonpapillate.

Remarks. All the leaf remains are fragmentary, not more than 10 mm long. The entire length could be up to 30 mm. The maximum breadth of the leaf blade is in the upper quarter,

tapering rapidly to the rounded, shortly mucronate apex that distinguishes the species from the small-leaved *Pseudotorellia*, such as *P. minuta, P. tjukansis* and *P. angustifolia* [2-5]. Keel in *P. angustifolia* is not a permanent feature. *P. kharanorica* differs further from the latter species in scattered stomata not forming definite intercostal stomatal bands as well as in the microsinuate epidermal walls. In most *Pseudotorellia* species, subsidiary cells are strongly papillate.

Material. Abundant leaf fragments from coal beds and overlying tuffs; Kharanor mine, Transbaikalia; Kharanor Suite, Lower Albian.

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LEAF WHORLS OF CUPRESSACEAE FROM THE MAASTRICHTIAN OF CENTRAL KAZAKHSTAN

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Abstract. This is the first description of cupressaceous leaves, from the Maastrichtian of Kazakhstan, with diagnostic micromorphological features such as Florin rings and papillae. The micromorphological evidence suggests their affinities with several taxa such as *Chamaecyparis, Thujopsis, Libocedrus* as well as *Thuja*. The micro- and macromorphological features reflect the transitional nature of the Late Cretaceous forms.

В коллекции из маастрихтских отложений Аркалука обнаружены хорошо сохранившиеся обрывки побегов кипарисовых, сопоставимых с *Thuja, Calocedrus, Libocedrus* и *Chamaecyparis*. Номенклатурный статус *Cupressinocladus* остается неясным.

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The collection of gymnosperm and angiosperm compressions from the Maastrichtian beds of Nizhniy Ashut-I Quarry near Arkalyk, Turgay District, Central Kazakhstan, was made in 1986 by S. G. Zhilin and A. G. Andreev. Their age was determined by the spore and pollen assemblage as Upper Cretaceous (Maastrichtian).

Description

The plant remains are from a light gray gypsite kaolinic clay. Fossilized cupressaceous branchlets from 0.5 to 2.5 cm long are preserved as terminal whorls. The good preservation of compressions enables their investigation under LM and SEM (pl. I, figs. 1, 2). The leaf whorl is slightly appressed and branchlets are flattened. Scale leaves are densely crowded, imbricate, in opposite and decussate pairs, of two weakly differentiated types: an obtusely ovate-triangular median facial pair (1.5 mm), and a more rhombic lateral pair (1.5 mm) (pl. I, figs. 1, 2). On the upper third of the facial leaves, fossil resin glandule is very distinctive (fig. 1).

Cuticle details. Cuticle is amphistomatic. The stoma (pl. II, figs. 1, 2; pl. III, fig. 3) is cyclocytic or subamphicyclocytic 71 μm long and 43 μm wide. Guard ceils (pl. III, figs. 1, 3) are

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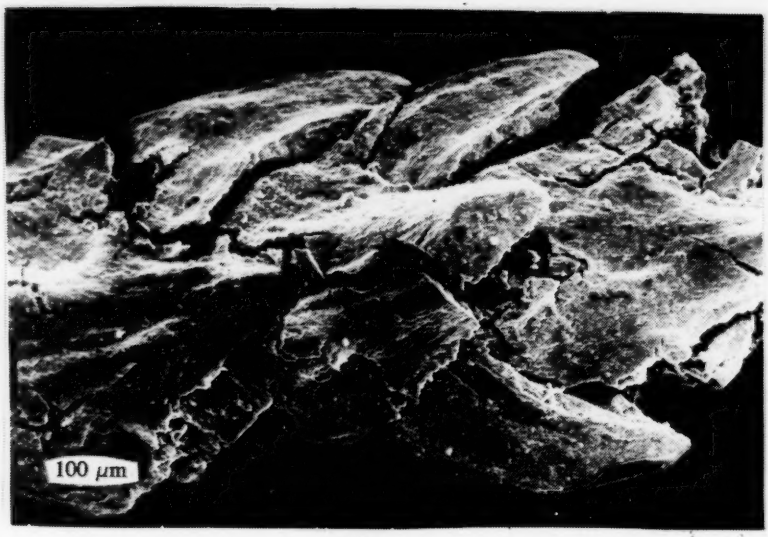

Fig. 1

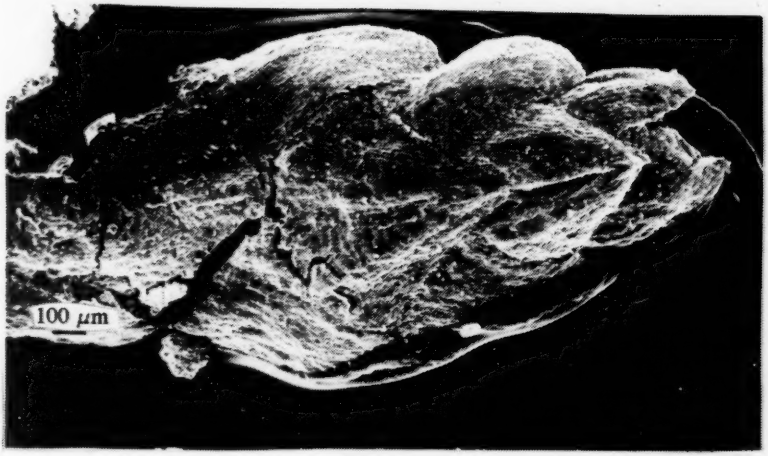

Fig. 2

PLATE I

sunken, 10-14 μm long. Orientation of stomatal aperture is parallel to epidermal rows, rarely random, and 15 μm long in both cases. There are 4-6 subsidiary cells, typically 5, which cover the stomatal aperture to form a stomatal pit (pl. II, figs. 1, 2). Near the border of the pit, the thickened cuticle forms an elliptical Florin ring, 27 μm long and 13 μm wide (pl. III. figs. 1, 3). On the rim, papillae originate from subsidiary cells. Papillae are present on the outer periclinal walls (pl. III, figs. 1-3) of epidermal cells. The papillae are hollow, a single papilla is 4-6 μm in diameter (pl. IV). Occasionally two stomata come in contact with each other and share their subsidiary cells (pl. II, fig. 1). Subsidiary cells are slightly different from interstomatal epidermal cells. Characteristic features of the leaf cuticle of our leafy shoots are as follows: (1) it is amphistomatic; (2) stomatal complex is subamphicyclocytic, i.e., adjacent subsidiary cells are slightly differentiated from interstomatal epidermis; (3) two adjacent stomata share subsidiary cells; and (4) hollow papillae are present on the periclinal walls of ordinary epidermal cells (in rows, as well as interstomatal).

Discussion

The above features are distinctive for some *Cupressinocladus*, assigned to Cheirolepidiaceae [10]. For example, a feature such as sharing a subsidiary cell in adjacent stomatal apparatus is a character of cupressoid shoots, e.g., *Thujopsis dolabrata* (L.F.) Siebold et Zucc. Hence, the specimen is referred to Cupressaceae because of general morphology of the leaf whorl. As is evident in this discussion, the gross morphology of Late Cretaceous leaves of Cupressaceae may not be sufficient reason for ascertaining their relationship to modern taxa [2, 17]. The combination of characters found in the fossil foliage is unknown in any one modern genus or species of Cupressaceae. Similar shoots with scalelike leaves in whorls are found in extant *Chamaecyparis, Libocedrus*, as well as *Thuja* and *Thujopsis*. Admittedly, a diagnostic character such as the cuticle anatomy of the leaves is known in this fossil taxon and is essential for a complete comparison with extant Cupressaceae. Without this knowledge and meticulous analysis with SEM of characters of extant Cupressaceae species, it is only speculation to place the fossils in the same modern genus as *Thula, Chamaecyparis*, or any Cupressaceae. The species usually identified as *Thula cretacea* (Heer) Newb. was first found in Kazakhstan as an anatomically well-preserved leaf compression. Such a morphotype could be easily tested, by external morphology, on widely distributed floras of the northern hemisphere, mostly in Late Cretaceous and less often in Early Paleogene. Another name for the species is *Cupressinocladus cretacea* (Heer) Sew., whose genus was established by Seward [13]. Its type species is *C. salicornioides* (Ung.) Sew., based on *Thuites salincornioides* Ung. However, such a nomenclatural typification

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KEY TO PLATE I

Thuja cretacea. SEM view of gross form of foliage shoots (fragments) showing the opposite decussate leaf arrangement.

Fig. 1. Central part of shoot, No. 113, *a*; ×40.

Fig. 2. Apex of shoot; No. 113, *b*; ×40.

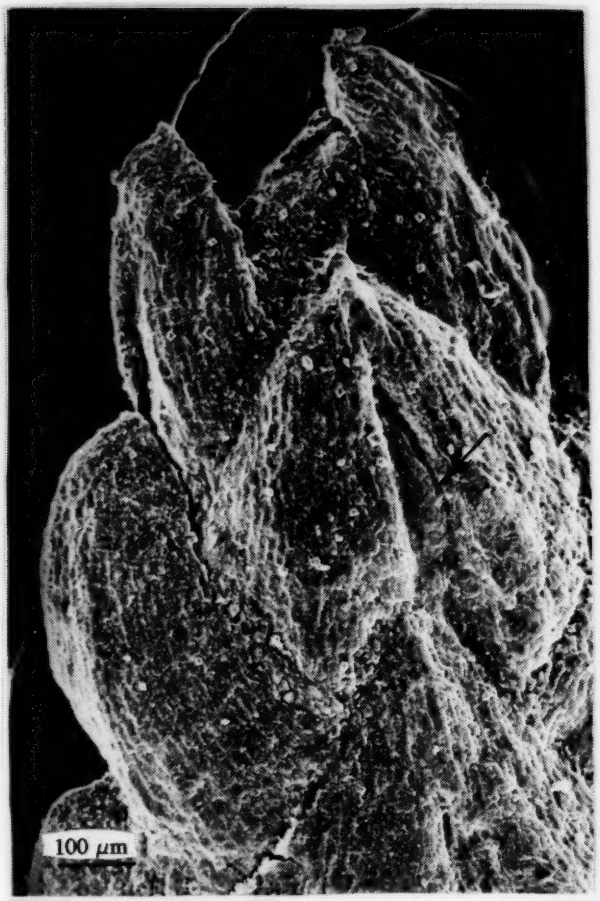

Fig. 1. *Thuja cretacea*. Apex (SEM) of shoot with preserved resin glandulae (see arrow): leaves with stomata and epidermal cells, No. 113, *b*; ×100.

of the Mesozoic (Jurassic and Cretaceous) genus *Cupressinocladus* should not be *Thuites salicornioides*, a Late Tertiary species; it is usually referred to such extant genera of Cupressaceae as *Libocedrus* and *Calocedrus*, also to different synonyms such as *Hellia* and *Heyderia*, as well as to the Tertiary form genera *Thuites* and *Libocedrites*. Recently, Z. Kvacek [8] referred it to *Tetraclinis*, suggesting that the Jurassic and Cretaceous genus *Cupressinocladus* should be considered extinct. In assigning our specimen to *Thuja cretacea* and deriving the specific name "*cretacea*" from *Cupressinocladus*, we are neither making a decision on the range and value of the genus nor establishing the age limit for the extant *Thuja* to the beginning of the Late Cretaceous. We are simply identifying the specimen by a broadly known name and pointing out the sufficient resemblance with the extant genus *Thuja*.

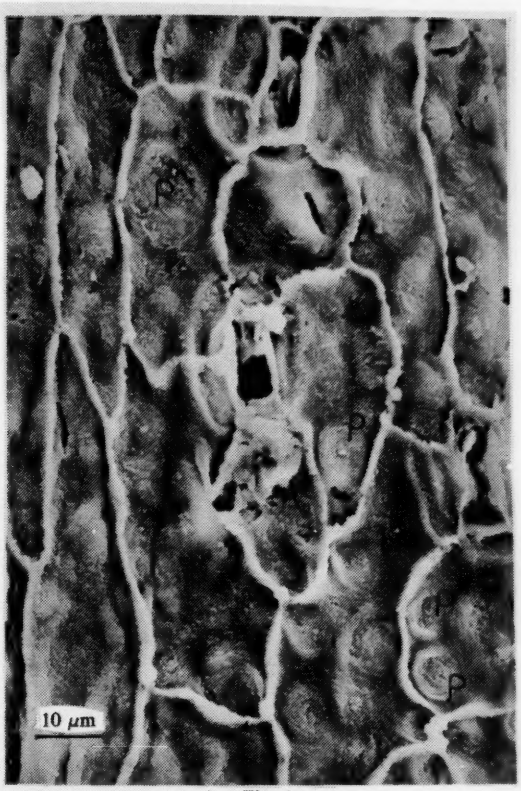

Fig. 1

Fig. 2

PLATE II

KEY TO PLATE II

Thuja cretacea. Epidermal structure.

Fig. 1. Internal view of cuticle surface (SEM): stoma with subsidiary cells slightly differentiated from interstomatal epidermal cells, No. 113, *c*; ×1000. P - papillae.

Fig. 2. Abaxial epidermis of the leaf (LM): stoma and epidermal cells, No. 113, *c*; ×400.

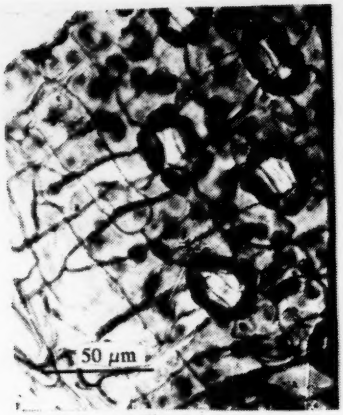

Fig. 1

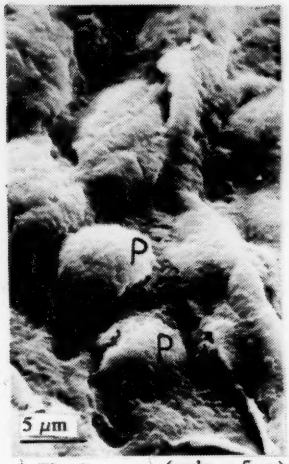

Fig. 2 (scale = 5μm)

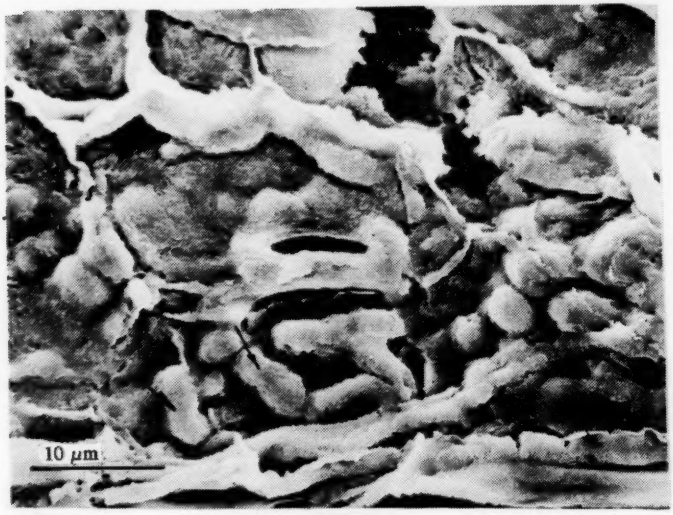

Fig. 3

PLATE III

KEY TO PLATE III

Thula cretacea. Epidermal structure.

Fig. 1. Adaxial epidermis of the leaf (light micrograph): Florin rings and papillae surrounding the stomata, No. 113, *c*; ×400.

Fig. 2. External view of cuticle surface: papillae (SEM), No. 113, *c*; ×2000. P - papillae.

Fig. 3. Sculptured periclinal surface with Florin rings adjacent to papillae forming cristae (see arrows), No. 113, *c*; ×1000.

Thuja cretacea (Heer) Newb.

Fig. 1; Pls. I-IV

Thuja cretacea (Heer) Newberry, 1895 [9]: 53, pl. 10, figs. 1, 1*a*; Kryshtofovich, 1938 [6]: 10, fig. 7; pl. 1, figs. 5, 6; Kryshtofovich and Baykovskaya, 1960 [7]: 65, fig. 23; pl. 13, figs. 6, 7; Sveshnikova, 1967 [15]: 198, pl. 11, figs. 9-11; pl. 12, figs. 1-4; Sveshnikova and Budantsev, 1969 [16]: 86, pl. 34, figs. 7-20; Samylina, 1988 [12]: 78, pl. 29, figs. 1-12; pl. 30, figs. 12, 13.

Libocedrus cretacea Heer, 1882 [3]: 49, pl. 29, figs. 1-3; pl. 43, fig. 11.

Cupressinocladus cretacea (Heer) Seward, 1926 [14]: 100; Krassilov, 1979 [5]: 102, pl. 19, fig. 5-8; pl. 23, figs. 1-6.

Cupressinocladus sveshnikovae Ablaev, 1969 [1]: 1411, fig. s.n.; pl. s.n., figs. 1-13.

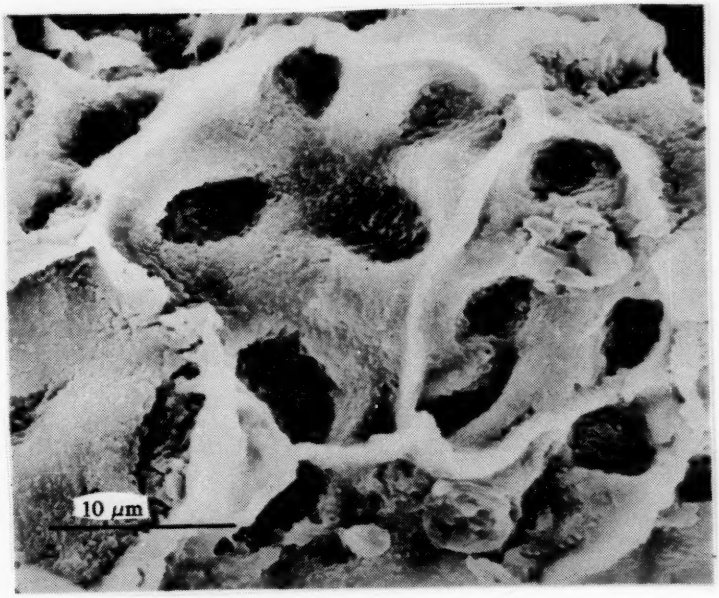

PLATE IV

KEY PLATE IV

Thuja cretacea. Apex (SEM) of shoot with preserved resin glandulae (see arrow): leaves with stomata and epidermal cells, No. 113, *b*; ×100.

Our leafy shoots of *Thuja cretacea* are the first well-preserved compressions of Cupressaceae from Kazakhstan [17]. In external appearance they resemble a recently collected *T. cretacea* from the Upper Cretaceous of Kazakhstan [11] and another from the Lower Paleocene of Raychikha (Zeya-Bureya depression, Kivda Formation) [4], both fossils with no preserved cuticles. It should be noted that leafy shoots with preserved cuticles (LM) and adjacent attached cones from the east Siberian Vilyuy depression [16] were assigned to *T. cretacea*. The cupressoid species from the Maastrichtian of Central Kazakhstan is between some *Chamaecyparis* and *Libocedrua* on the one hand, and *Thuja* and *Thujopsis* on the other. Different types of Florin rings and papillae structures as well as subsidiary cells should be scrupulously analyzed in extant Cupressaceae in order to assign fossils to the same modern genus. The combination of characters in fossils is intermediate, which reflects transitional nature of archaic forms.

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Alapaja (TAXODIACEAE) SEEDS FROM THE CENOMANIAN-TURONIAN OF NORTHERN KAZAKHSTAN

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Abstract: This is the first study of one of the richest collections of Late Cretaceous seeds, fruits and other plant remains from northern Kazakhstan. The Cenomanian-Turonian Shet-Irgiz Formation of clay and sand is present in the iron quarries (Sokolovka and Sarbay). Among numerous plant remains are undoubted taxodiaceous seeds, *Alapaja* Dorof., and, possibly, *Taxodiastrum* Dorof. and *Quasisequoia* Friis.

В Сарбайском карьере, Северный Казахстан, найдены структурно сохранившиеся остатки листьев, семян и плодов, среди которых анатомически изучены семена таксодиевых, отнесенные к ископаемому роду *Alapaja*.

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In 1969, S. G. Zhilin made a rich collection of cones, seeds, scales and fruits of conifers, and fruits and seeds of angiosperms from the Cenomanian-Turonian beds of the Shet-Irgiz Formation [3, 4], not far from Kustanay (Sarbay Quarry, near Rudnyy, northern Kazakhstan). In 1992 we began to study this collection, using morphological and anatomical methods of P. A. Nikitin [2] and P. I. Dorofeev [1] with light [LM] and scanning electron (JSM-35) [SEM] microscopes.

The first species identified was *Alapaja uralensis* Dorof. (Taxodiaceae)[1]. Our seeds are black with matte surface and correspond to the protologue (fig. 1).

Alapaja uralensis Dorof.

Figs. 1-8; Pls. I, II

Alapaja uralensis Dorof. 1979 [1]: 314, fig. 1, 8-10; fig. 3, 5-8; fig. 7, 1-10.

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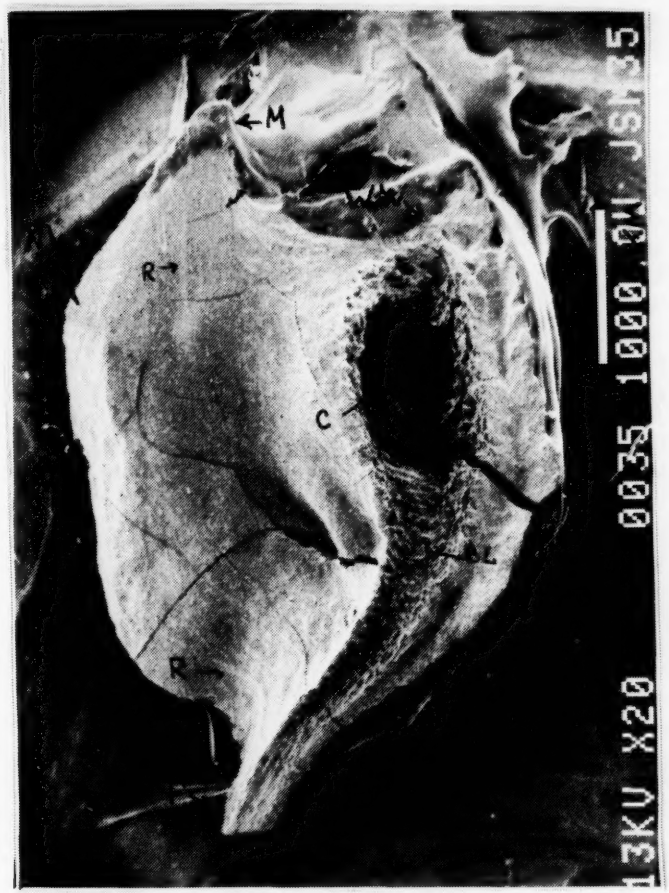

Fig. 1. *Alapaja uralensis*. General view of seed (×20 SEM): R - ribs, C - cavity, BL - break-line, M - micropyle, F - funiculus, WW - wide wing, NW - narrow wing, RW - rib of narrow wing.

P. I. Dorofeev (1911-1985) described this genus and species from the Cenomanian-Turonian near Alapayevsk (Sverdolovsk District). He described the seeds of *Alapaja* as being 2.7-5.0 × 1.8-2.45 mm, oval, and curved along the longitudinal section (fig. 1). The top narrows into a micropylar knob (figs. 1, 7-M) and curved to the back. The base is cuneiform and consists of a short or long central funiculus (figs. 1, 7-F).

The seeds are pressed to the back having the even border and are supplied with the undulate crest (fig. 1 UCr).

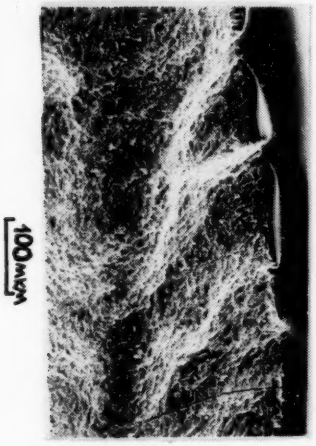

Fig. 1

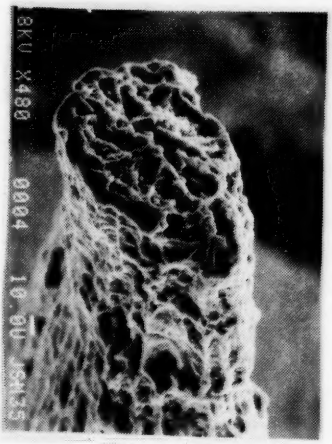

Fig. 2

Fig. 3

Fig. 4

PLATE I

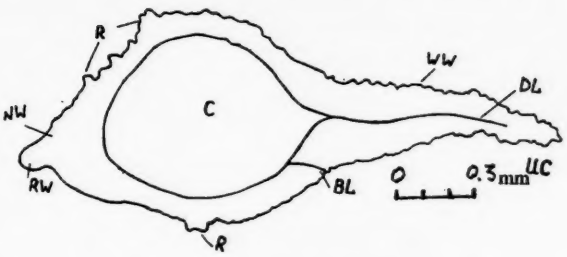

Fig. 2. Cross section of closed seed (×20).

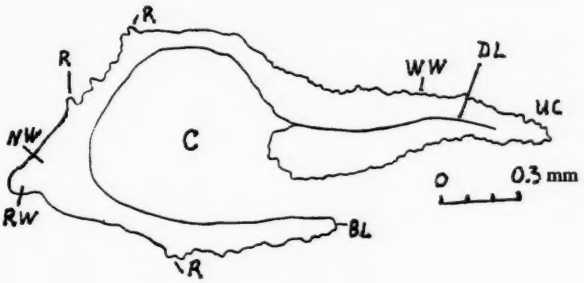

Fig. 3. Cross section of open seed (×20); for other designations, see figs. 1, 2. Parts of fig. 3 are seen on figs. 4-6.

The narrow break-line (BL) is along the abdominal side from the seed's upper end to the funiculus base. Sometimes, on the lower seed surface, narrow and sharp ribs (fig. 1-R) along the back are seen. The cavity (fig. 1-C) of the seed is curved.

However, our *Alapaja* seeds are different—they are larger than Dorofeev's seeds (3.0-7.0 × 1.7-4.0 mm). Also, the anatomical investigations of our seeds (Coll. 1700a, No. 1) indicate that Prof. Dorofeev was not quite correct. We think that the seed's asymmetry is connected with the inequality of two wings that are in the tangential plane (figs. 2, 3-WW, NW). It is not quite correct to name their position as "back" and "abdominal" sides.

KEY TO PLATE I

Figs. 1-4. *Alapaja uralensis*. Parts of fig. 1; for designations, see fig. 4 in text: fig. 1 - ribs on undulate crest (×100 SEM); fig. 2 - structure of micropyle surface (×240 SEM); fig. 3 - surface of exotesta (×180 SEM); fig. 4 - surface of sclerotestas (×180 SEM).

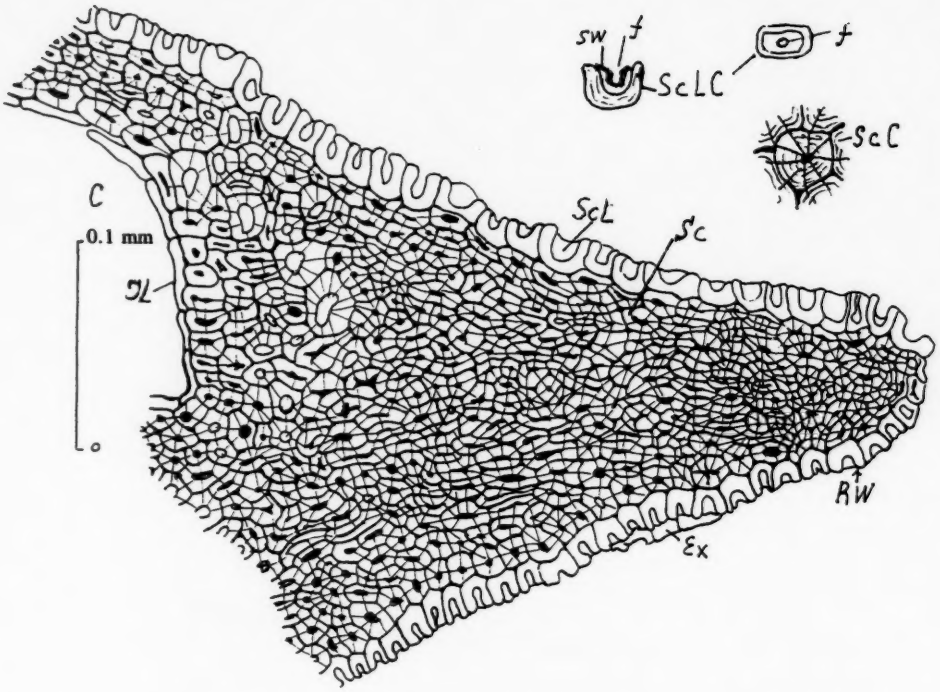

Fig. 4. Cross section of the narrow wing: Ex - exotesta layer, Sc - sclerotesta layer, ScC - sclerotesta cells, ScL - sclerotesta outer layer, ScLC - sclerotesta outer layer cells, BLC - break-line cells, IL - inner layer of thin-walled cells, sw - thin and concave outer wall, f - round cells' flexure in this wall; for other designations, see figs. 1, 2.

As seen in figures 2 and 3, the narrow wing (NW) (width 0.36 mm) has a triangular cross section. At 0.15 mm from the cavity it is sharply transformed into the narrow rib (width (0.1 mm). Another wing (WW) is wide (1.0-1.5 mm), slim (0.1-0.4 mm), and flat with a curved end. It has an undulate surface and toothed border (pl. I, fig. 1), because of featherlike ribs (fig. 1; pl. I, fig. 1 - UCr).

Ours and Dorofeev's seeds are open (figs. 1 and 3). As seen in cross section (fig. 6), one side of the wide wing comes from the seed. The break-line is formed on the longitudinal thin-walled cells extending across the wall of the seed's cavity (fig. 6, BLC). It is probable that they opened during germination.

In the SEM (pl. I, fig. 3 - Ex) the upper layer cells (the so-called exotesta) are big with thin walls (100-130 μm long, thickness of wall - 5-7 μm). These cells are seen on some cross sections of the seed (fig. 6; pl. II, figs. 1-4 Ex). On the micropylar apex of seed, these cells are 10-20 μm long (pl. I, fig. 2). This layer is not always preserved on the entire surface, and Dorofeev pointed out that it was not preserved on his sections. This layer is very transparent,

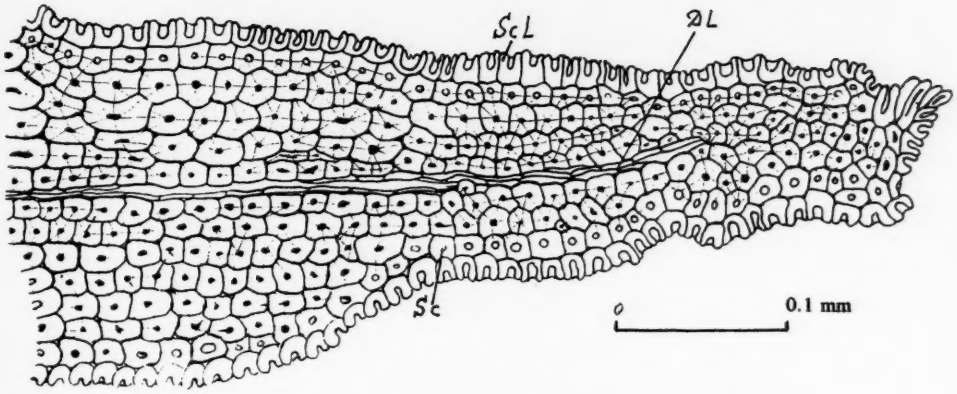

Fig. 5. Cross section of wide wing; for other designations, see fig. 4.

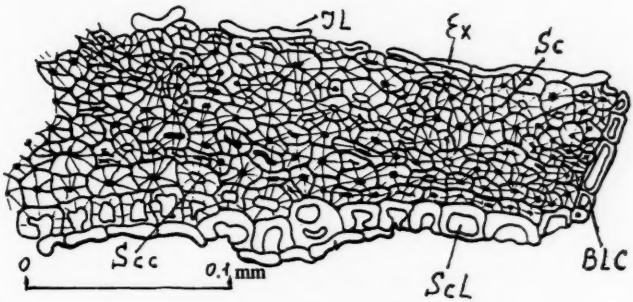

Fig. 6. Cross section of wall of seed cavity: Scc - second outer angular cells with big cavities; for other designations, see fig. 4.

and the next layer—the outer layer of the so-called sclerotesta (the middle layer of seed's skin) (pl. I, figs. 3, 4 - Sc)—can be seen through it. It consists of small square or right-angled cells (d = 14-25 μm).

As seen in figures 4-6 the radial and tangential inner walls of these cells are thick, and the outer wall is slim and concave. Such cells appear damaged and open, but the micrograph and drawing demonstrate the presence of an outer wall that is crumpled and with a round central flexure (d = 11 μm) (fig. 4 - sw, f).

The rest of the sclerotesta is formed by very thick-walled cells and surrounds the entire seed cavity.

The narrow wing consists of large (d = 15-25 μm) cells (fig. 4). They are round, ovate,

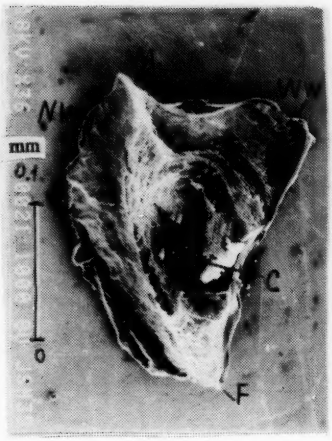

Fig. 7. General view of dissected seed (×18 SEM); for designations see fig. 1.

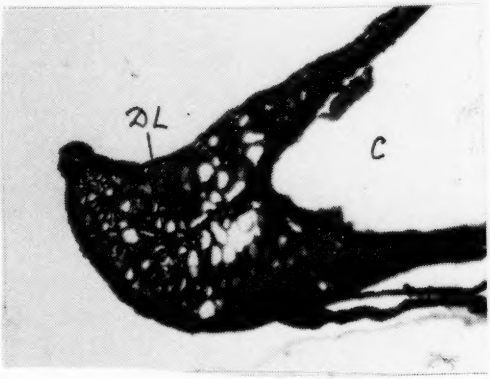

Fig. 8. Cross section of wing of *Sequoiadendron giganteum* (Lindl.) Buchh. (×20 LM); for designations, see fig. 2.

or angular in cross section, and with such thick walls that cavities are absent. The cell walls have pores and their flexed structure is seen in the sections (fig. 4).

The wide wing (fig. 5) consists of the same thick-walled cells, in 7-12 rows. A narrow dark line is in the middle of the wing (fig. 5 - DL) and is similar to "seam" in the wings of *Sequoiadendron* seeds (fig. 8). This "line" consists of cells with thin walls extending along the wing, and resembling the break-line thin-walled cells (figs. 2, 3, 6 - BL, 5 - DL).

Fig. 1

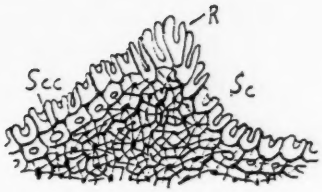

Fig. 2

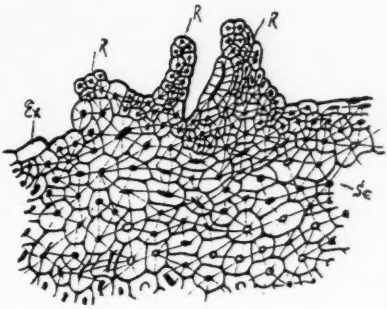

Fig. 3

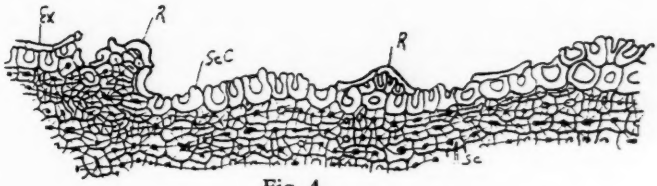

Fig. 4

PLATE II

KEY TO PLATE II

Figs. 1-4. *Alapaja uralensis*. Cross sections of different types of ribs on outer surface on upper part of seed.

In the wall of the cavity (0.1-0.18 mm thick) under the outer layer is one row of angular cells with big cavities and medium thick walls (fig. 6 - Scc).

The rest of the sclerotesta consists of homogenous ovate thick-walled cells, with narrow fissurelike cavities distributed along the seed cavity.

The cavity border layer consists of damaged slim walls and extended cells that are similar to the wing's line cells.

The ribs on the seed surface of different types, sizes, and forms, and consists of rows of thick-walled cells, some of which are covered by exotesta (pl. II, figs. 1-4).

In conclusion, it should be noted that our detailed anatomical investigations, despite some difference with Dorofeev, confirm that our seeds belong to *Alapaja uralensis* Dorof. We have analyzed in greater detail the morphology of this taxon, and have succeeded in finding new anatomical details confirming their relation to extant Taxodiaceae.

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NEW SPECIES OF *Aquilapollenites* POLLEN FROM THE LOWER MAASTRICHTIAN OF THE FAR EAST

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Abstract. New species *Aquilapollenites striatus* Markevich from the Lower Maastrichtian of Primor'ye and Amur resembles the North American species *A. stelkii* Srivastava, but differs in the striation pattern. Stratigraphy and paleoecology of the "unica" pollen producers are discussed.

Новый вид *Aquilapollenites striatus* из нижнего маастрихта Приморья и Амурской области близок *A. stelkii* из маастрихта Сев. Америки, но отличается характером штриховатости. Обсуждается стратиграфия и палеоэкология продуцентов пыльцы unica.

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Aquilapollenites pollen grains occur in the upper Turonian to lower Paleocene [1, 5, 6]. Geographically they range from northern Siberia and Spitsbergen to India, Kalimantan [Borneo], and South America.

The pollen-producing plants transgressed provincial boundaries defined both palynologically and by macrofossils [1, 2, 6]. These distributional features suggest pioneer plants of a very broad adaptational niche. In the Far East they are less prominent than in contemporaneous deposits of western Siberia or the American midcontinent. Perhaps they preferred open coastal plains to the montane landscapes that have prevailed in the Far East since mid-Cretaceous time [2].

Morphologically, *Aquilapollenites* suggests entomophilous pollination strategy. It shows diverse equatorial projections and surface sculpturing consisting of variously shaped striae and spinules. Their pattern is used for paleopalynological classification that reveals great taxonomic diversity: no less than 50 species in North American assemblages, and about 40 species in contemporaneous Asiatic assemblages [3, 4, 6].

Pollen grains of a new species, *Aquilapollenites striatus*, are from two localities in Primor'ye and Amur. In the Zoyechkin Kljuch locality, Muraveyka River basin, south Primor'ye, the Maastrichtian pollen assemblage was obtained from exploratory shafts and wells Nos. 8-3, 9, 1310-1-2, 1336-1, 1336-2-1, 1342, 1360, and 3815, drilled through the sequence of alternating sandstones, shales, tuffs, and thin coals resting on porphyritic rocks. The spore-pollen assemblage

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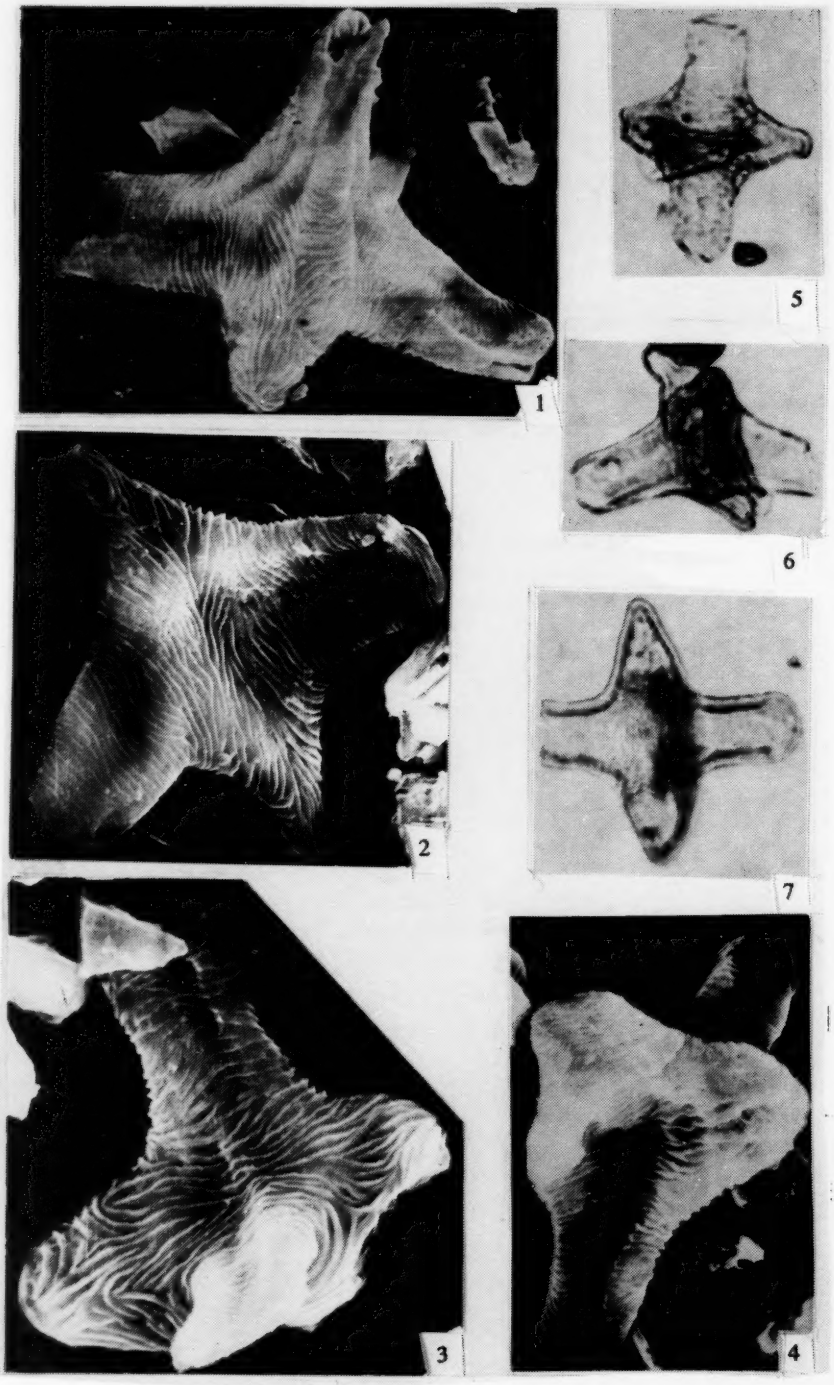

PLATE I

contains abundant *Laevigatosporites ovatus* Wilson et Webster; common *Retitriletes austroclavaditites* (Cookson) Krutzch, *Stereisporites antiquasporites* Dettmann, *Osmundacites wellmanii* Couper, *Baculatisporites concinus* (Cookson) Potonie, *B. comaumensis* Dettmann; rare *Nevesisporites radiatus* Chlonova, *Cicatricosisporites dorogensis* Potonie et Gelletich, *Divisisporites euskichensoides* Thomson, *D. enormis* Pflug, *Gleicheniidites senonicus* Ross, *Radialisporites radiatus* (Krutzch) Krutzch, and *Leiotriletes* spp.

Taxodiaceous pollen grains constitute about 20% of the gymnosperms. They are represented by *Taxodiumpollenites distichiforme* (Simpson) Srivastava, *T. hiatus* (Potonie) Kremp, *Inaperturopollenites dubius* (Potonie et Gelletich) Thomson. The bisaccate group includes *Abietinaepollenites varius* Norton, *Pinuspollenites parvus* Norton, *P. ellepticus* Cookson, *Piceapollenites* sp., *Cedruspollenites obscura* Zauer, *Podocarpidites magnus* (Simpson) Srivastava, and *P.* sp. Occasional grains are assigned to *Gnetaceaepollinites multicostatus* (Brenner et Norris) Verbizkaia and *Vitreisporites pallidus* (Reissinger) Nilson. *Classopollis* is absent.

Angiosperms mostly belong to the "unica" and " oculata" groups. Dominant genera are *Aquilapollenites* (*A. asper* N. Mchedlishvili, *A. cruciformis* N. Mchedlishvili, *A. quadrilobus* Rouse, *A. striatus* Markevich, *A. granulatus* N. Mchedlishvili, *A. conatus* Norton, *A. subtilis* N. Mchedlishvili, *A. dispositus* N. Mchedlishvili, *A. echinaceus* N. Mchedlishvili, *A. amurensis* Bratzeva), *Manicicorpus* (*M. anchoriforme* N. Mchedlishvili, *M. solidum* N. Mchedlishvili, *M. notabile* N. Mchedlishvili, *M. tenue* N. Mchedlishvili, *M. trapeziformis* N. Mchedlishvili, *M.* sp.), *Wodehouseia* (*W. spinata* Stanley, *W. elegans* Samoilovich, *W. gracilis* (Samoilovich) Pokrovskaia), *Azonia* (*A. fabaceae* Samoilovich, *A. calvata* (Samoilovich) Wiggins) and *Syngularia* (*S. aculeata* Samoilovich). They are accompanied by *Orbiculapollis* (*O. globosus* (Chlonova) Chlonova, *O. lucidus* Chlonova), *Fibulapollis mirificus* Chlonova, as well as diverse tricolporate, triporate and tricolpate grains of *Retitricolpites vulgaris* (Pierce) Srivastava, *Tricolpites mataurensis* Couper, *T. foveolatus* Norton, *T. striatellus* N. Mchedlishvili, *Tricolpopollenites microreticulatus* Norton, *Triporopollenites radiatostriatus* (N. Mchedlishvili) Bratzeva, *T. robustus* Pflug, *T. mullensis* (Simpson) Rouse et Srivastava, *Triatriopollenites plicoides* Zaklinskaia, *T. confusus* Zaklinskaia, and *Syncolpites porosus* N. Mchedlishvili.

The remaining angiosperm pollen grains are conventionally referred to extant families of Santalaceae: *Kuprianipollis elegans* (Zaklinskaia) Komarova, *K. santaloides* (Stelmak) Komarova, *Paliurus triplicatus* Anderson; Liliaceae: *Liliacidites mirus* Srivastava, *L. creticus* Couper, *L. variegatus* Couper, *L. curvimuratus* Srivastava, *L. morrinensis* Srivastava; Proteaceae: *Proteacidites crispus* Samoilovich, *P. convexiporus* Samoilovich, *P. formosus* Samoilovich, *P. angulatus* Samoilovich, *P. thalmanii* Anderson (most common), *Beaupreaidites elegansiformis* Cookson, *B. oculatus* (Samoilovich) Srivastava; Ulmaceae: *Ulmoideipites tricostatus* Anderson, *U. krempii*

KEY TO PLATE I

Aquilapollenites striatus sp. nov. from the Maastrichtian of Primor'ye, Far East: 1-4 - SEM micrographs showing characteristic striation, ×1000 and ×1500; 5-7 - light micrographs showing nexinal extensions into equatorial projections, ×600.

Anderson (summarily about 20%); Loranthaceae: *Cranwellia striata* (Couper) Srivastava, *Loranthacidites macrosolenoides* N. Mchedlishvili, *Erdmanipollis pachyzandroides* Krutzch, *E. albertensis* Srivastava; Betulaceae: *Triporopollenites bituites* (R. Potonie) Elsik, *Polyvestibulopollenites verus* (R. Potonie) Thomson et Pflug, *Carpinuspollenites* sp., *Coryluspollenites* sp.; Fagaceae: *Quercites sparsus* (Martynova) Samoilovich, *Quercuspollenites* sp., *Faguspollenites* sp., *Castaneapollenites* sp.; Platanaceae: *Platanuspollenites* sp.; Juglandaceae: *Juglanspollenites* sp., *Caryapollenites* sp., *Pterocaryapollenites* sp., *P. stellatus* (R. Potonie) Tiergarten, *Engelhardtiapollenites tenuipollis* (Anderson) Srivastava, as well as *Myricipites* sp., *Nyssapollenites* sp., *Acerpollenites* sp., *Salixpollenites* sp., *Rouseia subtilis* Srivastava and occasional grains of Hamamelidaceae, Araliaceae, Ericaceae, Moraceae, Bombacaceae, Rutaceae and Oleaceae.

This assemblage is repeated with minor differences in the samples from the Kundur dinosaur locality, Amur Province, where *Aquilapollenites striatus* was found. Both localities show an association of dominant evergreen elements with subordinate broadleaf deciduous elements characteristic of Early Maastrichtian floras.

Aquilapollenites striatus Markevich, sp. nov.

Plate I, figs. 1-7

Holotype. No. 1336-1-4, Institute of Biology and Pedology (pl. I, fig. 1), Zoyechkin Kljuch, Muraveyka River, South Primor'ye, Lower Maastrichtian.

Diagnosis. Pollen grains iso- to subisopolar, equatorial aspect elliptical, with tapering, slightly asymmetrical points. Three equatorial projections, equal to or longer than extremities of body, slightly if at all tapering but distally expanded and rounded, emerging at open angle or nearly perpendicular to body. Exine thick, sexine tectate columellate, nexinal thickenings continuous from body to projections, distally vanishing. Colpi short, distinct. Surface sculpturing formed by fused sexinal clavate elements arranged in regular striate pattern over body and projections.

Dimensions (mm). Polar axis 36.2, equatorial axis 12.6, projection length 19.2, width 10.8.

Material. Eighteen grains from Zoyechkin Kljuch, Muraveyka River, South Primor'ye, and Kundur, Amur Province, Lower Tsagajan Suite; Lower Maastrichtian.

Comparison. *A. striatus* resembles *A. stelkii* from the Late Campanian-Maastrichtian of Alberta, Canada [6], in general configuration of the body and projections and their dimensions, but differ in the striation pattern extending over the body.

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CHARACTERS OF COLONIALITY IN DIATOMS

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Abstract. Developmental studies have revealed four types of structures that indicate colonial habit — spines, spinules, ridges, and granules. Spines link valves in colonies, as in *Aulacoseira italica*, and are of fairly constant shape. Spinules develop on the valve margins, and assist in linking cells, but their shapes and dimensions are variable, as in *Diatoma hiemale*. Ridges occur on the valve margins in pennate forms as low serrate siliceous outgrowths, e.g., in *Didymosphenia geminata*. Granules are produced on the contact surfaces in combination with other elements or alone. These types of contact structures correlate with longevity of the colonies.

Описаны четыре типа соединительных структур – шипы, шипики, гребни и гранулы, развивающиеся на контактах клеток, образующих временные колонии. Показано, что различные типы контактных структур указывают на длительность существования колоний.

• • •

Many diatoms form colonial aggregates with hard or mucous links, or both. Form of the colony can be constant for a species or variable, depending on environmental factors [4].

Coloniality is an important taxonomical character (incidentally distinguishing structurally similar *Synedra* and *Fragilaria* [11]), which is often not directly observable even in extant material. A lot of single cells in planktonic assemblages are derived from benthic or periphytonic colonies. Many colonies disperse during preparation for study, and usually the colonial aggregates do not withstand the standard study treatment for diatom analysis. It is quite evident that fossil assemblages are strongly biased in respect to colonial forms.

In this paper I describe characters which can be potentially useful in recognizing colonial adaptations in fossil diatoms. In the extant diatom genera that form permanent colonies, three types of marginal structures are absent in the noncolonial unicells—spines, ridges and granules.

The first type includes both the connective spines typically developed in the centric diatoms such as *Aulacoseira* [1] (pl. I, fig. 1) and the spinules occurring on the margins of contacting valves in *Diatoma, Fragilaria, Tabellaria*, and some other genera (pl. I, figs. 3-6, 9-11; see also [5, 11]).

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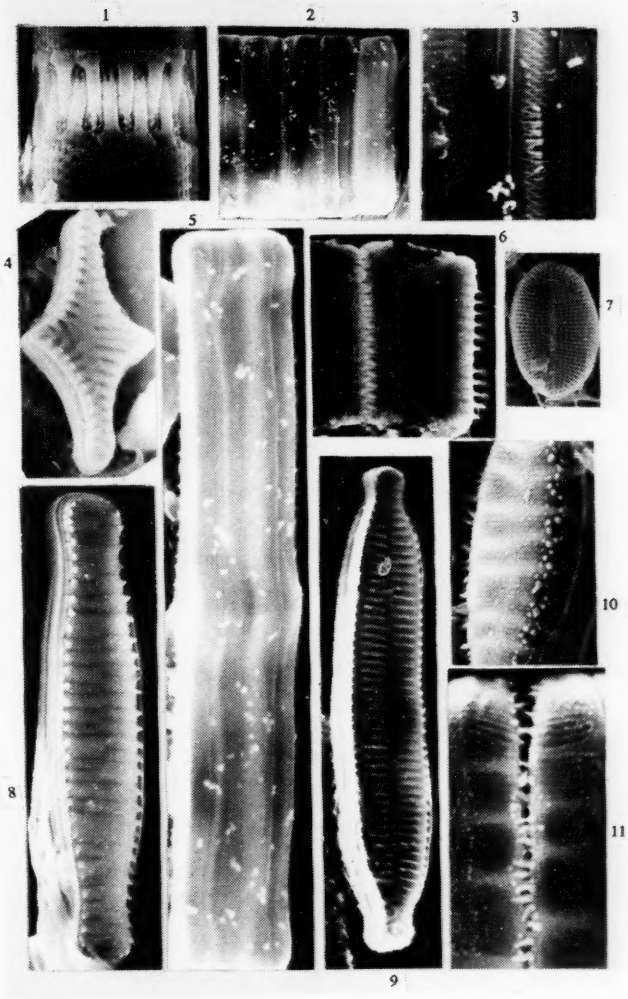

PLATE I

KEY TO PLATE I

Types of cell contact structures, SEM.

Fig. 1. Connective spines, *Aulacoseira italica*, ×3500.

Figs. 2-6, 8-11 - spinules; **2-3** - *Fragilaria virescens*, ×800, ×5000, **4** - *F. leptostauron*, ×1500; **5** - *Tabellaria fenestrata*, ×1500; **9** - *Hannaea arcus* var. *linearis f. recta*, ×3000; **6** - *F. virescens* var. *oblongella*, ×2400; **10, 11** - *Diatoma hiemale* var. *mesodon*, ×2400, ×4600; **8** - *D. vulgare*, ×2500.

Fig. 7. Valve of *Cocconeis placentula* without characters of colonial structure, ×2500.

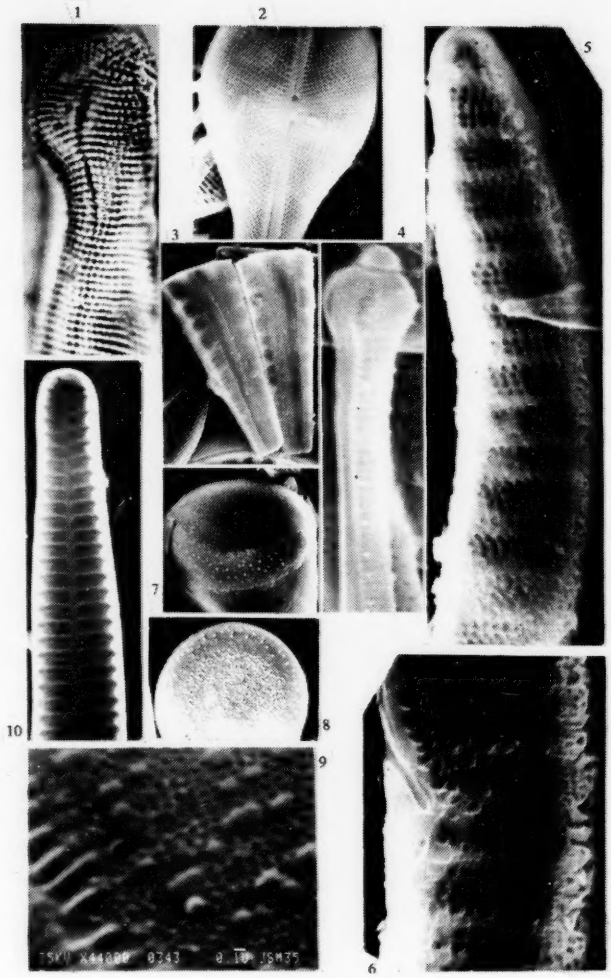

PLATE II

KEY TO PLATE II

Types of cell contact structures, LM, SEM.

Figs. 1, 2, 5, 6, - ridges. 1, 2 - *Didymosphenia geminata*: 1 - LM, ×1700; 2 - SEM, ×1200; 5, 6 - *Epithemia zebra* var. *porcellus*, SEM, ×3000 and ×5000.

Figs. 3, 4, 7, 8, 9 - granules; 4 - *Asterionella formosa* SEM, ×4500; 3 - *Meridion circulare*, SEM, ×1500; 7, 8, 9 - *Melosira varians*, SEM, ×2000, ×20000.

Fig. 10. *Synedra ulna*, without characters of colonial structure, SEM, ×4000.

Ridges occur marginally on the contacting valves of *Epithemia* and *Didymosphenia* (pl. II, figs. 1-2, 5, 6). Although largely overlooked, these features have occasionally been noticed in *Pleurosigma angulatum* and some other species having circular marginal projections [2, 7].

Granules have been observed in a number of species with (e.g., *Asterionella formosa*) or without (e.g., *Melosira varians*) other types of colonial characters (pl. II, fig. 3). In *M. varians* granules form marginal rings or central clusters (pl. II, figs. 7, 8, 9). In *Aulacoseira italica* granules fill the spaces between the connective spines (pl. I, fig. 1), while in *Diatoma hiemale* var. *mesodon* they occur between spinules as well as over the entire contacting surfaces of the valves (pl. I, figs. 10, 11).

Apparently the granules are the most common structures, resulting from the exchange of siliceous compounds between the contacting silica-organic thecae or even between the layers within the thecae. The latter suggestions agree with the occurrence of granules at the contact of the coating membrane (cingulum) [3, 10] and the basal layer in *A. italica* (pl. I, fig. 1). The fibrous basal layer in *Melosira varians* (pl. II, figs. 7, 8, 9) may have similar origin.

Various types of colonial structures seem to have been correlated with stability (longevity) of the colonial aggregates. Thus, spines occur in diatoms, forming stable colonies [9] capable of withstanding fossilization and subsequent treatment. Less durable colonies are formed by cells with marginal spinules of variable shape and dimensions as in *Fragilaria* (pl. I, figs. 2-4). Even less stable are colonies with marginal spinules formed as conical projections on the marginal ridges, e.g., in *Diatoma* (pl. I, fig. 8), *Tabellaria* (pl. I, fig. 5) or *Semiorbis hemicyclus* [6]. In addition to the thecal connective structures, these species have mucous connections secreted by projections of porose fields at the cell ends [8].

Ridge structures occur in association with transitory coloniality. For instance, in *Didymosphenia* cell valves contact each other for a short time only, after which they diverge into a dichotomously branched colony on mucous stalks. *Pinnularia*, with marginal ridges was occasionally reported to form lenticular colonies [12], although these are absent in our material.

Granules are not to be considered as connective structures although they are constantly associated with coloniality in the cells connected by coating membranes, as in *Melosira varians*. Such colonies can be more-or-less stable, depending on the growth rates and environmental factors.

In conclusion, the characters regularly associated with coloniality in diatoms result from the exchange of organic silica compounds between contacting cells. Their types reflect duration of the contacts, thus correlating with stability of the colonial aggregates.

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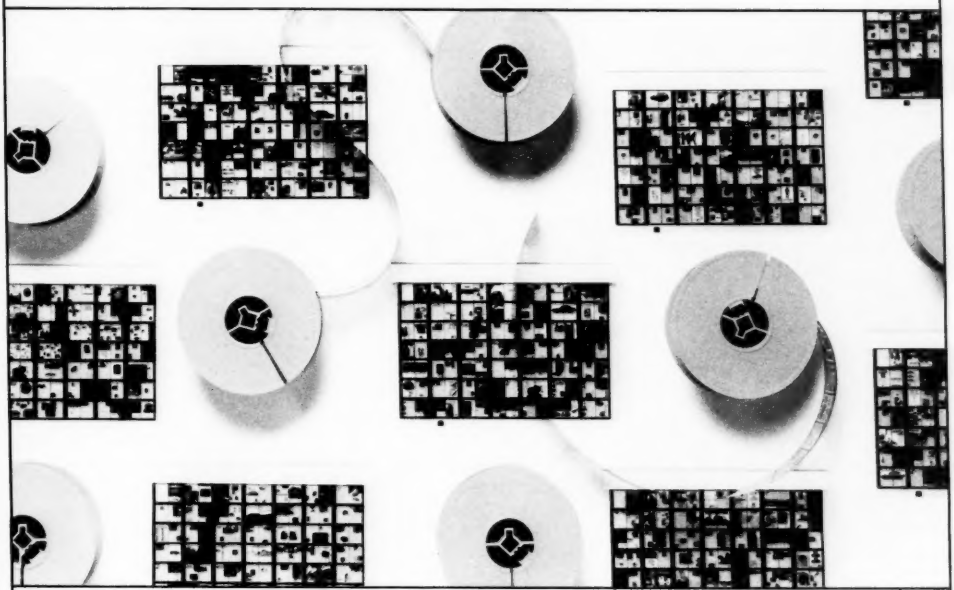

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